SYSTEMATIC REVISION AND PHYLOGENY OF *PASPALUM* SUBGENUS *CERESIA* (POACEAE: PANICOIDEAE: PANICEAE)[1]

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ABSTRACT

Twenty-five species are treated in this work, in which exomorphological characters are analyzed cladistically. Species of *Paspalum* subg. *Ceresia* are characterized by their rigid, filiform to lanceolate blades, inflorescences with one to several racemes, rachis of the racemes winged and hyaline to membranous, spikelets pilose, occasionally glabrous, with the upper anthecium pale, hyaline to membranous, occasionally chartaceous, and the upper lemma not enclosing the tip of the upper palea. Species grow in South America from Mexico to Argentina and Uruguay. A cladistic analysis of subgenus *Ceresia* was conducted to test its monophyly, and to establish its relationship with other groups of *Paspalum*. A key to the species in subgenus *Ceresia* is given, as well as morphological description and illustration, and distribution maps.

Key words: America, *Ceresia*, cladistics, *Paspalum*, Poaceae.

Paspalum L. includes approximately 330 species distributed in tropical and subtropical regions of America, with a few taxa growing in the Old World (Clayton & Renvoize, 1986). Due to its large number of species, and the morphological variation present within the genus, *Paspalum* has been divided into subgenera, sections, or informal groups mainly on the basis of morphological characters, such as inflorescence type or features of the spikelet (Nees, 1829; Doell, 1877; Chase, 1927; Pilger, 1929; Clayton & Renvoize, 1986; Morrone et al., 1995, 1996, 2000; Cialdella et al., 1995).

Chase (1929) divided *Paspalum* into subgenera *Paspalum* and *Ceresia* (Pers.) Rchb., characterizing the latter by its foliaceous rachis, with one to several racemes per inflorescence and spikelets densely pilose, with long white hairs, mainly along the margins of the upper glume and lower lemma.

Taxonomic studies in *Ceresia* are fragmentary; with respect to the subgenus, these *Paspalum* species have been analyzed in regional works or floral treatments (Nash, 1912; Chase 1927, 1929; Pilger, 1929; Hitchcock, 1951; Burkart, 1969; Rosengurtt et al., 1970; Sendulsky & Burman, 1978, 1980; da Silva et al., 1979; Pohl, 1980; Judziewicz, 1990; Renvoize, 1998; Rodríguez, 1998).

The present taxonomic treatment revises *Paspalum* subg. *Ceresia*, considering vegetative and reproductive characters, analyzing habitat and distribution range. A cladistic analysis was further performed in order to test the monophyly of the subgenus and to establish the relationships of its species.

HISTORY

Ceresia was established at the generic level by Persoon (1805–1807), on the basis of *C. elegans* (= *Paspalum membranaceum* Lam., non Walt., 1788). Subsequently, Reichenbach treated *Ceresia* as a subgenus of *Paspalum* (Chase, 1929). Several species were described in *Ceresia* in the 19th century (Flüggé, 1810; Trinius, 1826, 1828–1836, 1834; Nees, 1829; Doell, 1877).

Nees (1829) considered, within *Paspalum*, section *Digitaria*, including *P. pectinatum* and species currently treated in *Axonopus*; section *Lanigeri*, including *P. eucomum*, *P. guttatum*, *P. erianthum*, *P. sanguinolentum*, *P. ammodes*, *P. polyphyllum*, and *P. blepharophorum* (= *P. polyphyllum*); and sections *Cristati*, *Genuini*, *Axonopodes*, and *Ceresiae*, with *P. pyramidalis* (= *P. repens*) and *P. stellatum*.

Doell (1877) grouped *Paspalum* into three sections: sect. *Eremachyrion*, sect. *Emprosthion*, and sect. *Opistion*, including in section *Opistion* the fol-

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lowing species: *Paspalum aspidiotes* (subg. *Ceresia*), *P. pectinatum* (subg. *Ceresia*), *P. eucomum* (subg. *Ceresia*), *P. blepharophorum* (= *P. humboldtianum*, subg. *Ceresia*), *P. ammodes* (group Eriantha), *P. guttatum* (group Eriantha), *P. sanguinolentum* (group Eriantha), *P. erianthum* (group Eriantha), *P. stellatum* (subg. *Ceresia*), *P. membranaceum* (= *P. ceresia*, subg. *Ceresia*), *P. heterotrichon* (subg. *Ceresia*), *P. trachycoleon* (subg. *Ceresia*), *P. lanciflorum* (subg. *Ceresia*), and *P. carinatum* (subg. *Ceresia*).

Bentham (1881) considered three sections in *Paspalum*: sect. *Anastrophus*, sect. *Cabrera*, and sect. *Eupaspalum*, the first two characterized by the presence of distichous spikelets with the lower lemma facing the axis, while in section *Eupaspalum* spikelets are unilateral with the lower lemma outward from the axis of the raceme. Within section *Eupaspalum*, Bentham (1881) distinguished four subsections: subsect. *Anachyris*, as an artificial group with a single bract below the upper anthecium; subsect. *Ophistion*, with species without a foliaceous rachis; subsect. *Seudoceresia*, with a rachis more or less foliaceous, green, and concave with glabrous and small spikelets (including such species as *P. stoloniferum* and *P. repens*); and subsect. *Ceresia*, characterized by its foliaceous rachis, with the margins membranous and colored, spikelets ciliate and larger. Within subsection *Ceresia*, Bentham included many tropical species and also *P. cymbiforme*.

Pilger (1929) divided *Paspalum* into eight sections: sect. *Eupaspalum*, sect. *Anachyris*, sect. *Pterolepidium*, sect. *Erianthum*, sect. *Cymatochloa*, sect. *Ceresia*, sect. *Eriolepidium*, and sect. *Moenchia*. This author treated in section *Ceresia* such species as *P. membranaceum* (= *P. ceresia*), *P. stellatum*, *P. heterotrichon*, *P. carinatum*, *P. eucomum*, *P. pectinatum*, *P. cordatum*, *P. humboldtianum*, and *P. trachycoleon*.

Chase (1929), in her study of North American species of *Paspalum*, related subgenus *Ceresia* with her group Dissecta, both with the rachis of the racemes foliaceous and winged, separating Dissecta by the presence of glabrous spikelets. Among the species included by Chase in her treatment are: *Paspalum pectinatum*, *P. contractum* (= *P. lanciflorum*), *P. stellatum*, *P. heterotrichon*, *P. trachycoleon*, *P. cymbiforme*, and *P. humboldtianum*. Chase (1929) stressed that *P. sanguinolentum* (excluded here) did not belong to subgenus *Ceresia* but to group Eriantha. Later, Chase (ined.) placed in subgenus *Ceresia P. carinatum*, *P. ceresia*, *P. heterotrichon*, *P. stellatum*, *P. trachycoleon*, *P. phyllorhachis*, *P. soboliferum* (= *P. humboldtianum*), *P. polyphyllum*, *P. humboldtianum*, *P. humboldtianum* var. *stuckertii* (= *P. humboldtianum*), *P. buchtienii*, *P. malmeanum*, *P. eucomum*, *P. splendens* (= *P. eucomum*), *P. guttatum*, and *P. ammodes*. On the other hand, *Paspalum aspidiotes*, *P. pectinatum*, *P. cordatum*, *P. setiglume*, *P. contractum*, and *P. lanciflorum* were grouped in section *Pectinata* (see Table 4 for groups considered here).

Clayton and Renvoize (1986) recognized eight sections within *Paspalum*: sect. *Diplostachys*, sect. *Pterolepidium*, sect. *Anachyris*, sect. *Erianthum*, sect. *Eriolepidium*, and sect. *Moenchia* with a triquetrous, not membranous, rachis; sect. *Paspalum* and sect. *Ceresia* with a membranous or foliaceous, winged rachis. Section *Ceresia* was distinguished (Clayton & Renvoize, 1986) by including species with a membranous, colorful rachis, and spikelets with the upper glume and lower lemma scabrous, usually ciliate, sometimes winged.

Rodríguez (1992) established *Paspalum* sect. *Pectinata* and distinguished it from section *Ceresia* by including species with spikelets winged and broadly ovoid, cordiform or not at the base.

Filgueiras and Davidse (1994) described, within *Paspalum* subg. *Ceresia*, section *Biaristata*, including two species: *P. biaristatum* and *P. longiaristatum*, both defined by conspicuous awns on the upper glume and lower lemma.

Most recently, Rodríguez (1998) made an account of nine species of *Paspalum* subg. *Ceresia* for Venezuela: *P. setiglume*, *P. pectinatum*, *P. lanciflorum*, *P. carinatum*, *P. humboldtianum*, *P. polyphyllum*, *P. stellatum*, *P. trachycoleon*, and *P. heterotrichon*, all with a winged rachis and pilose spikelets.

MATERIALS AND METHODS

MORPHOLOGICAL ANALYSIS

Specimens were examined from the following herbaria: B, BAA, BM, COL, CONC, CTES, G, IBGE, K, LE, LIL, LPB, MA, MEXU, MO, P, R, RB, SI, UB, US, W (Holmgren et al., 1990; Appendix 2). A list of specimens examined for the outgroup taxa is provided in Appendix 3. Scanning electron micrographs (SEMs) were prepared of the upper anthecium of six species, utilizing the procedures described by Soderstrom and Zuloaga (1989). The vouchers for this SEM study are marked with an asterisk in Appendix 2; the type specimen of *P. reticulinerve*, *Solomon 17003*, was also used. The specimens were viewed on a Zeiss 940 A scanning electron microscope of the Darwinion institute, operating at 10–20 kV.

PHYLOGENETIC ANALYSIS

Characters. Fifty-eight exomorphological characters were used in the cladistic analysis; 15 char-

Table 1. Morphological characters and character states used for the cladistic analysis of *Paspalum* subg. *Ceresia*.

Life form

1. Life cycle: perennial (0), annual (1). This character is a synapomorphy for group Racemosa in *Paspalum*. Annual species in section *Ceresia* are *Paspalum longiaristatum* and *P. cachimboense*.
2. Habit: terrestrial (0), aquatic or subaquatic plants (1).
3. Culms with spongy pith: absent (0), present (1).

Both characters 2 and 3 are helpful to solve relationships within the outgroup.

Blades

4. Shape: linear-lanceolate (0), linear (1).
5. Basal leaves: not pseudopetiolate (0), shortly pseudopetiolate (1), markedly pseudopetiolate (2). *Paspalum buchtienii*, *P. cymbiforme*, and *P. humboldtianum* have shortly pseudopetiolate leaves, with the pseudopetiole a narrowed zone at the base of the blade. Markedly pseudopetiolate leaves is an autapomorphy for *P. imbricatum*, where leaves have a long narrowed zone between the collar and the flattened blade, both about the same length.

Inflorescenses

First-order branching of species here treated in *Panicum* and *Anthaenantiopsis* are considered homologous to unilateral racemes in *Paspalum*.

6. Spikelets unilaterally arranged on the rachis: absent (0), present (1). Unilaterally arranged spikelets are present in all studied species of *Paspalum*.
7. Truncate inflorescences: absent (0), present (1). The inflorescence is truncate when its main axis does not end in a spikelet, and the most distal raceme is a first order branch.
8. Raceme number per inflorescence: 1 (0), 2 (1), 3 or more racemes (2).
9. Arrangement of racemes: solitary (0), conjugate (1), subdigitate (2), alternate (3). Racemes are conjugate when the internode between two contiguous racemes is almost absent; when these internodes are short, up to 1 cm long, racemes are subdigitate; finally, when the internodes are well developed, racemes are considered as alternate.
10. Rachis of the racemes: triquetrous (0), winged with longitudinal veins at the wings (1), winged with anastomosed veins at the wings (2), winged and nerveless, with hyaline to membranous wings (3). The rachis was scored as triquetrous when the ventral side has the same development of the lateral margins, while it was considered as winged when the lateral margins are clearly developed and flat. Nerveless and hyaline to membranous wings only occurs in some species of *Paspalum* subg. *Ceresia*.
11. Rachis of the racemes: ending in a spikelet (0), in a naked point (1), in both a spikelet or in a naked point (2). Within subgenus *Ceresia*, and group Racemosa in *Paspalum*, the rachis usually ends in a sterile prolongation. Nevertheless, the rachis ends both in a spikelet or in a naked point in several species of the subgenus, while in *P. goyasense* it always ends in a developed spikelet.
12. Rachis disarticulating at maturity: absent (0), present (1). This character is a synapomorphy of the Racemosa group.

Table 1. Continued.

13. Pedicels laterally inserted in the spikelets: absent (0), present (1). This feature is present in *Paspalum heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis*, where a scar is noticeable at the lateral base of the upper glume (Fig. 1F, 2F).

Spikelets

14. Shape: biconvex (0), plano-convex (1). Plano-convex spikelets are a synapomorphy within the studied species of *Paspalum*.
15. Disposition: solitary (0), paired (1), paired with the lower spikelet reduced or aborted (2), with 3 or more spikelets together (3). When the inner spikelet is reduced or aborted, evidence of the paired condition is seen in the presence of the lower pedicel. Two, three, or more spikelets are present on one branch in *Panicum laxum* and *P. obtusum*.
16. Spikelets with an annular thickening at the base: absent (0), present (1). This character is present in *Paspalum heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis*.

Lower Glume

17. Presence: present (0), absent (1). The lack of a lower glume is a synapomorphy of the studied species of *Paspalum*.

Upper glume

18. Texture: hyaline (0), membranous (1). We consider the upper glume as hyaline when light passes through it, and membranous when it does not.
19. Winged upper glume: absent (0), present (1). A winged upper glume has flat and extending margins. This character is shared by species of section *Pectinata*, with the exception of *Paspalum lanciflorum* and *P. cachimboense*.
20. Base cordate: absent (0), present (1). As in the previous character, this feature is present in section *Pectinata* (but not in *Paspalum lanciflorum* and *P. cachimboense*).
21. Apex: not awned (0), awned (1). Awned glumes are present in *Paspalum longiaristatum* and *P. biaristatum*.
22. Corky margins: absent (0), present (1); usually found in *Paspalum buchtienii*, *P. cymbiforme*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*.
23. Ciliate margins: absent (0), present (1). We consider that the margins are ciliate when they have short, rigid, and setose hairs in only one series, *Paspalum reticulinerve* and *P. aspidiotes*.
24. Pilose margins: absent (0), present (1). Marginal hairs are long, not rigid, and arranged in several series.
25. Radiate marginal hairs: absent (0), present (1). When marginal hairs are radiate, they look like a crown, as in *Paspalum buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*.
26. Surface pilosity: absent (0), hairs basal, arising from a basal point (1), hairs present in the lower half of the upper glume (2), hairs all over the surface of the upper glume (3). Hairs are usually found in *Paspalum* subg. *Ceresia* in the basal portion and margins of the upper glume; they are less frequent in the distal portion.

Table 1. Continued.

27. Numbers of nerves: 2 (0), 3 (1), 5 (2), 7 (3).
28. Disposition of nerves: equidistant (0), lateral nerves near the margins (1). This character is helpful to resolve relationships within outgroups.
29. Position of lateral nerves: marginal (0), submarginal (1).
30. Lateral extension of the margins: flat (0), curved after the nerve (1), plicate along the nerve (2), absent (3). We considered a lateral extension present when the margin continues after the lateral nerve.
31. Marginal nerves only present in the lower half of the upper glume: absent (0), present (1). This is a common character for species of section *Pectinata*, with the exception of *Paspalum lanciflorum* and *P. cachimboense*.
32. Anastomosed veins in the upper glume: absent (0), present (1). This is a character observed in *Paspalum reticulinerve* and *P. aspidiotes*.
33. Base horseshoe-shaped: absent (0), present (1). This is observed in *Paspalum buchtienii* and *P. humboldtianum*, both species with basal margins extended.

Lower floret

34. Lower floret: present, staminate (0), absent (1). The absence of a lower floret is a synapomorphy of *Paspalum*.

Lower lemma

35. Texture: hyaline (0), membranous (1).
36. Wings: absent (0), present (1). Wings on the lower lemma were considered present when the margin of the lower lemma is flat and extended, as in *Paspalum reticulinerve*, *P. imbricatum*, and *P. aspidiotes*.
37. Base: rounded (0), subcordate (1), cordate (2). A cordate lower lemma was observed in *Paspalum imbricatum* and *P. aspidiotes*, while it is subcordate in *P. pectinatum* and *P. cordatum*.
38. Apex: not awned (0), awned (1). An awned apex of the lower lemma is found in *Paspalum longiaristatum* and *P. biaristatum*.
39. Ciliate margins: absent (0), present (1). As in character 23, the lower lemma margins are considered ciliate when these appendages are short, rigid, setose, and arranged in one series along the margins, as in *Paspalum reticulinerve* and *P. aspidiotes*.
40. Margin pilosity: absent (0), present (1).
41. Tuberculate, marginal hairs: absent (0), present (1). This is a character observed in *Paspalum lanciflorum*, *P. cachimboense*, *P. pectinatum*, and *P. cordatum*.
42. Surface pilosity: absent (0), present (1).
43. Number of nerves: 2 (0), 3 (1), 5 (2).
44. Disposition of the nerves: equidistant (0), lateral nerves near the margins (1). This character is helpful to resolve relationships within outgroups.
45. Disposition of lateral nerves: marginal (0), submarginal (1).
46. Lateral extension of the margins: flat (0), curved after the nerve (1), plicate along the marginal nerve (2), absent (3). See character 30.
47. Marginal nerves only present in the lower half of the lower lemma: absent (0), present (1). One or two marginal nerves, which do not reach the apex, are present in *Paspalum imbricatum* and *P. aspidiotes*.

Table 1. Continued.

48. Relative length of upper glume and lower lemma: both bracts of the same length (0), upper glume longer (1), lower lemma longer (2).

Upper anthecium

49. Shape: ovoid to lanceolate (0), obovoid (1).
50. Stipe: absent (0), present (1). A stipe is present in *Paspalum lanciflorum*, *P. cachimboense*, *P. aspidiotes*, and *P. stellatum*.
51. Texture: hyaline (0), membranous (1), chartaceous (2).
52. Upper palea gap at the apex: not gaping, when the upper lemma encloses the apex of the palea (0), gaping, when the apex of the palea is free (1). All species of *Paspalum* subg. *Ceresia* have an open upper anthecium.
53. Relative length of the anthecium and the spikelet: equal (0), upper anthecium shorter than the spikelet (1).
54. Papillae at the upper lemma: absent (0), simple papillae (1), verrucose papillae (2). A simple papilla is an epidermic prominence including the cellular lumen, and a verrucose papilla is a papilla with additional prominences on the surface (Arriaga, 1987). Verrucose papillae are found in *Paspalum guttatum*, in the Eriantha outgroup, and in some specimens of *P. stellatum* within *Paspalum* subg. *Ceresia*.
55. Silica bodies at the upper lemma: absent (0), present (1).
56. Unicellular macrohairs at the upper lemma: absent (0), present (1).
57. Bicellular microhairs at the upper lemma: absent (0), present (1).
58. Lodicules: present (0), absent (1). Lodicules are absent in *Paspalum ceresia*, *P. longiaristatum*, and *P. biaristatum*.

acters are multistate and were treated as unordered; 11 of these characters were uninformative since they did not show variation within the ingroup. Table 1 provides the list of characters used in the analysis. Autapomorphies were excluded from the analysis. The data matrix is shown in Table 2. Some potentially informative characters were left out of the analysis, either because of the large amount of intraspecific variation, the lack of enough material, or because it was extremely difficult to score them due to overlapping states in different species, e.g., spikelet length and width, rachis width, and blade pilosity.

Cladistic analysis. The cladistic analysis was based on maximum parsimony using NONA version 2.0 (Goloboff, 1997a) under equal weights. Due to the large number of terminals, a heuristic analysis was run following command sequence: "hold10000; rseed 0; hold/40; poly = ; amb-; mult*100; max*; sswap*." One hundred subsearches were performed, each constructing a Wagner tree using a random addition sequence, swapping the initial tree with TBR

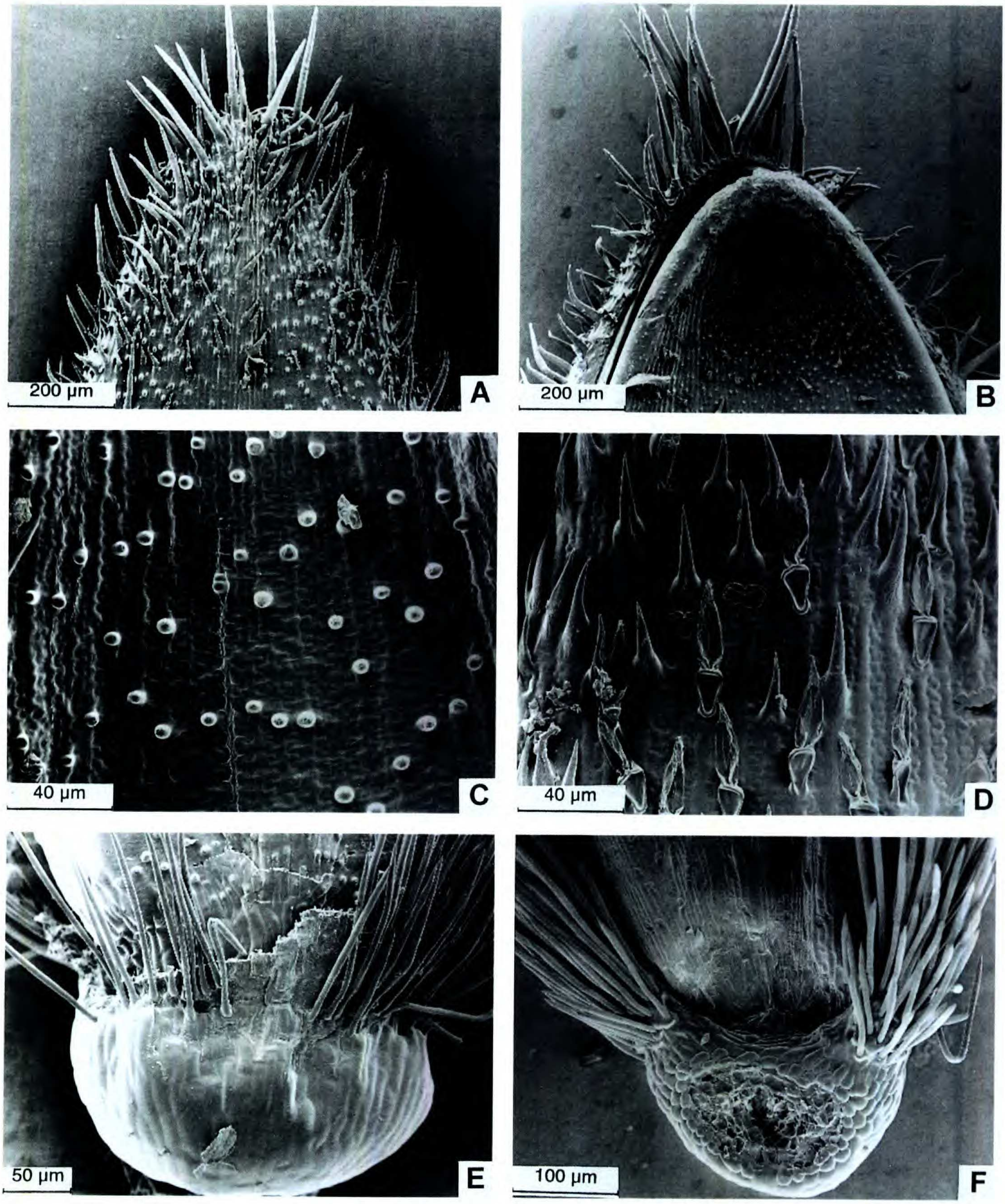

Figure 1. Scanning electron micrographs of the upper anthecium of *Paspalum*.—A. *P. pectinatum*, apex of the upper lemma (*Dusén 16057*, SI). —B. *P. reticulinerve*, apex of the upper palea (*Solomon 17003*, MO). —C. *P. trachycoleon*, upper palea with simple papillae (*Tamayo 2046*, US). —D. *P. biaristatum*, upper palea with bicellular microhairs, macrohairs (*Oliveira 758*, SI). E, F. *P. trachycoleon*.—E. Spikelet base, dorsal view (*Tamayo 2046*, US). —F. Spikelet base, ventral view (*Filgueiras 3567*, SI).

(tree bisection-reconnection) and retaining a maximum of 40 trees in each replication. The resulting trees were swapped using one round of TBR (max*) and one round of "sswap*," which performed TBR swapping cutting two sister nodes simultaneously. The default option "amb-" retained only nodes that are supported by unambiguous optimizations, while poly = treats trees as polytomous.

Table 2. Data matrix used in the cladistic analysis. Polymorphic character states are scored as: A = [01]; B = [02]; C = [03]; D = [12]; E = [23]; F = [012]; G = [013]; H = [023]; I = [123]. Dashes indicate character inapplicable for a taxon.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Panicum laxum	0	0	0	0	0	1	0	2	3	0	0	0	0	0	G	0	0	1	0
Panicum obtusum	0	0	0	0	0	0	0	2	3	0	0	0	0	0	G	0	0	1	0
Anthaenantiopsis fiebrigii	0	0	0	0	0	1	0	2	3	0	0	0	0	0	1	0	0	1	0
Paspalum acuminatum	0	1	1	0	0	1	1	F	H	1	0	0	0	1	0	0	1	0	0
P. almum	0	0	0	0	0	1	1	D	I	1	0	0	0	1	0	0	1	1	0
P. candidum	1	0	0	0	0	1	1	2	3	2	1	1	0	1	0	0	1	—	—
P. cromyorrhizon	0	0	0	1	0	1	1	D	2	0	0	0	0	1	0	0	1	1	0
P. dissectum	0	1	1	0	0	1	1	2	3	2	0	0	0	1	0	0	1	A	0
P. erianthum	0	0	0	0	0	1	1	2	E	1	0	0	0	1	1	0	1	0	0
P. guttatum	0	0	0	1	0	1	1	F	F	1	0	0	0	1	0	0	1	1	0
P. notatum	0	0	0	0	0	1	1	D	D	0	0	0	0	1	0	0	1	1	0
P. prostatum	1	0	0	0	0	1	1	2	E	2	1	1	0	1	0	0	1	1	0
P. racemosum	1	0	0	0	0	1	1	2	E	2	1	1	0	1	0	0	1	1	0
P. sanguinolentum	0	0	0	0	0	1	1	D	3	1	0	0	0	1	2	0	1	1	0
P. aspidiotes	0	0	0	0	0	1	1	2	3	3	1	0	0	1	0	0	1	1	1
P. biaristatum	0	0	0	1	0	1	1	F	C	3	1	0	0	1	0	0	1	0	0
P. buchtienii	0	0	0	0	1	1	1	2	E	1	2	0	0	1	2	0	1	A	0
P. burmanii	0	0	0	0	0	1	1	2	3	2	2	0	0	1	1	0	1	1	0
P. cachimboense	1	0	0	0	0	1	1	F	2	3	1	0	0	1	0	0	1	1	0
P. carinatum	0	0	0	1	0	1	1	A	C	3	1	0	0	1	0	0	1	1	0
P. ceresia	0	0	0	A	0	1	1	F	C	3	1	0	0	1	0	0	1	A	0
P. cordatum	0	0	0	1	0	1	1	2	2	1	1	0	0	1	0	0	1	1	1
P. cymbiforme	0	0	0	0	1	1	1	F	C	3	1	0	0	1	2	0	1	A	0
P. eucomum	0	0	0	1	0	1	1	D	D	3	1	0	0	1	0	0	1	1	0
P. goyasense	0	0	0	0	0	1	1	F	C	3	0	0	0	1	0	0	1	1	0
P. heterotrichon	0	0	0	0	0	1	1	F	C	3	1	0	1	1	0	1	1	0	0
P. humboldtianum	0	0	0	0	1	1	1	D	3	1	2	0	0	1	2	0	1	0	0
P. imbricatum	0	0	0	0	2	1	1	D	E	3	1	0	0	1	0	0	1	1	1
P. lanciflorum	0	0	0	0	0	1	1	F	B	3	1	0	0	1	0	0	1	1	0
P. longiaristatum	1	0	0	1	0	1	1	F	C	3	1	0	0	1	0	0	1	0	0
P. malmeanum	0	0	0	1	0	1	1	A	A	3	1	0	0	1	0	0	1	1	0
P. niquelandiae	0	0	0	0	0	1	1	2	3	1	2	0	0	1	1	0	1	1	0
P. pectinatum	0	0	0	0	0	1	1	D	D	3	1	0	0	1	0	0	1	A	1
P. petrense	0	0	0	0	0	1	1	2	3	2	1	0	1	1	2	1	1	A	0
P. phyllorhachis	0	0	0	0	0	1	1	2	3	2	1	0	1	1	1	1	1	A	0
P. polyphyllum	0	0	0	A	0	1	1	F	C	2	2	0	0	1	2	0	1	0	0
P. reticulinerve	0	0	0	0	0	1	1	D	D	1	1	0	0	1	1	0	1	1	1
P. stellatum	0	0	0	1	0	1	1	A	A	3	1	0	0	1	0	0	1	1	0
P. trachycoleon	0	0	0	0	0	1	1	2	3	2	1	0	1	1	1	1	1	A	0

Tests to evaluate homoplasy were consistency index (CI) and retention index (RI) (Farris, 1989).

Two strategies were carried out in an attempt to find possible islands for MP trees (Maddison, 1991). First, command "jump*3" was used, which performs TBR swapping on trees up to 3 steps longer than initial trees (Goloboff, 1993). The second strategy was carried out using "hold/5; mult*400," which performed 400 independent searches beginning from different Wagner trees.

Bremer support (Bremer, 1994) and jackknife group frequencies (Farris et al., 1996) were conducted in order to calculate branch support with NONA. Commands used for Bremer support were "subN; hold1500; find*"; bsupport performing TBR swapping on preexisting trees, saving trees up to 4 steps longer at each round. Jackknife frequency values were calculated using the available instruction file for NONA, the JAK.RUN file. One thousand iterations were performed, randomly deleting 36% of the characters, with the search options "mult*5," and the FQ.EXE file was used to cal-

Table 2. Extended.

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39
0	0	0	0	0	0	0	D	0	1	1	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	3	0	1	1	0	0	0	0	1	0	0	0	0
0	0	0	0	1	0	3	2	0	1	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	0	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	1	0	0	0	0
1	0	0	1	0	0	0	3	0	1	0	1	1	0	1	1	1	2	0	1
0	1	0	0	1	0	1	1	0	0	3	0	0	0	1	1	0	0	1	0
0	0	1	0	1	1	2	1	0	1	2	0	0	1	1	1	0	0	0	0
0	0	1	0	1	1	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	1	1	0	0	3	0	0	0	1	0	0	0	0	0
1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	0	1	0	0
0	0	1	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	1	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	3	1	0	1	2	0	0	1	1	1	0	0	0	0
1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	1	2	0	0
0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0
0	1	0	0	1	0	1	1	0	0	3	0	0	0	1	1	0	0	1	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	0	1	0	1	2	0	0	0	1	1	0	0	0	0
1	0	0	0	0	0	0	D	0	1	0	1	0	0	1	1	0	1	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	3	1	0	1	2	0	0	0	1	1	0	0	0	0
1	0	0	1	0	0	0	3	0	1	0	1	1	0	1	1	1	0	0	1
0	0	0	0	1	0	1	A	0	0	3	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0

culate the majority rule consensus trees of the output (Goloboff, 1993).

Separate analysis using implied weights (Goloboff, 1993) was run in PeeWee version 3.0 (Goloboff, 1997b) using the same search strategies as in NONA. PeeWee weights characters according to how well they fit a specific tree. Homoplastic characters were downweighted in proportion to their number of extra steps. We used a medium concave function, K = 3.

Outgroups. In the present treatment we followed Nixon and Carpenter (1993) for selecting the outgroups. Species of *Paspalum* that share potential synapomorphies with those of subgenus *Ceresia* were included as outgroups: taxa of the Dissecta, Erianthia, Racemosa, and Notata groups in *Paspalum* were chosen because they share with subgenus *Ceresia* a wide rachis in the inflorescences (Chase, 1929, ined.; Morrone et al., 1995; Zuloaga & Morrone, in prep.). Therefore, *P. acuminatum* and *P. dissectum*, of group Dissecta, *P. erianthum*, *P. guttatum*, and *P. sanguinolentum* of group Erianthia, *P.*

Table 2. Continued.

Character	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Panicum laxum	0	0	0	D	0	1	1	0	0	0	0	D	0	0	0	0	1	0	0
Panicum obtusum	0	0	0	2	0	1	1	0	2	0	0	2	0	0	0	1	0	1	0
Anthaenantiopsis fiebrigii	1	0	1	2	0	1	1	0	2	0	0	1	1	0	1	1	1	1	0
Paspalum acuminatum	0	0	0	2	1	1	0	0	0	0	0	2	0	1	1	1	1	1	0
P. almum	0	0	0	2	1	1	2	0	0	0	0	2	0	1	1	0	0	0	0
P. candidum	0	0	0	1	0	1	0	0	—	0	0	D	0	0	1	1	0	0	0
P. cromyorrhizon	0	0	0	2	1	1	2	0	0	0	0	D	0	1	1	1	0	1	0
P. dissectum	0	0	0	2	1	1	1	0	0	1	0	2	0	0	1	1	0	0	0
P. erianthum	1	0	1	1	0	1	1	0	0	0	0	2	0	1	1	0	0	1	0
P. guttatum	1	0	1	1	0	1	0	0	0	0	0	2	0	1	2	1	0	1	0
P. notatum	0	0	0	2	1	1	2	0	0	0	0	2	0	1	1	0	0	1	0
P. prostatum	0	0	0	1	0	1	1	0	0	0	0	2	0	0	1	0	0	1	0
P. racemosum	0	0	0	1	0	1	1	0	0	0	0	2	0	1	0	1	0	0	0
P. sanguinolentum	1	0	1	2	1	1	1	0	0	0	0	2	0	0	1	1	0	1	0
P. aspidiotes	0	0	0	2	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0
P. biaristatum	1	0	1	1	0	0	3	0	1	0	0	1	1	1	0	0	1	1	1
P. buchtienii	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. burmanii	0	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0
P. cachimboense	1	1	0	1	0	1	2	0	0	0	1	1	1	1	1	0	1	1	0
P. carinatum	1	0	1	1	0	1	1	0	1	0	0	1	1	1	1	0	1	1	0
P. ceresia	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1
P. cordatum	1	1	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
P. cymbiforme	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. eucomum	1	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0
P. goyasense	1	0	1	1	0	1	1	0	A	0	0	D	1	1	1	0	1	0	0
P. heterotrichon	1	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	1	1	0
P. humboldtianum	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. imbricatum	0	0	0	2	0	1	0	1	B	0	0	1	1	1	1	0	1	1	0
P. lanciflorum	1	1	0	1	0	1	2	0	1	0	1	1	1	1	1	1	0	1	0
P. longiaristatum	1	0	1	1	0	0	3	0	1	0	0	1	1	1	0	1	1	1	1
P. malmeanum	1	0	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0
P. niquelandiae	0	0	0	1	0	1	1	0	0	0	0	D	1	0	1	0	0	1	0
P. pectinatum	1	1	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
P. petrense	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. phyllorhachis	0	0	0	1	0	1	2	0	0	0	0	1	1	0	1	0	1	1	0
P. polyphyllum	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0
P. reticulinerve	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0
P. stellatum	1	0	1	0	0	0	3	0	0	1	1	1	1	1	B	0	0	0	0
P. trachycoleon	0	0	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0

almum, *P. cromyorrhizon*, and *P. notatum* of group Notata, and *P. candidum*, *P. prostatum*, and *P. racemosum* of group Racemosa were included in the present analysis (Table 4).

Panicum obtusum Kunth and *Anthaenantiopsis fiebrigii* Parodi were also included as outgroups due to their relationship with *Paspalum*, stressed by a recent molecular analysis of the tribe (Giussani et al., 2001). Finally, for the purpose of rooting, *Panicum laxum* Sw., a C_3 representative of the $x = 10$ clade of the Paniceae (Giussani et al., 2001) was also considered in this analysis.

MORPHOLOGICAL CHARACTERS

Habit. Species of *Paspalum* subg. *Ceresia* are perennial, rarely annual (in *P. longiaristatum* and *P. cachimboense*). Culms are herbaceous, occasionally lignified (in *P. buchtienii* and *P. humboldtianum*), unbranched or branched at the lower and middle nodes, hollow, and erect or leaning on the vegetation. Blades range from filiform to linear or lanceolate; a short pseudopetiole is present in *P. buchtienii*, *P. humboldtianum*, and *P. cymbiforme*, while *P. imbricatum* is characterized by its long pseudopetiolate blades.

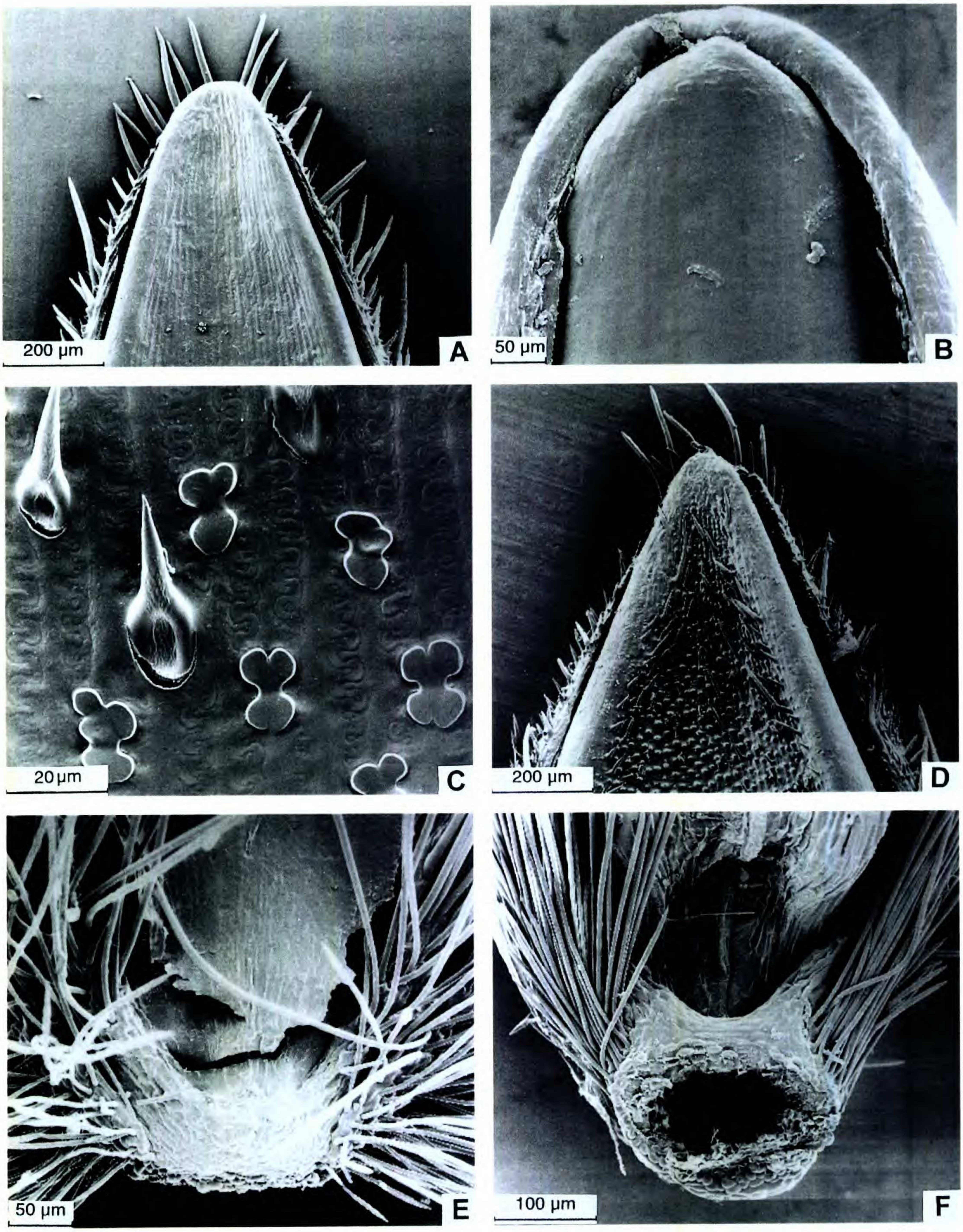

Figure 2. Scanning electron micrographs of the upper anthecium of *Paspalum*.—A. *P. pectinatum*, apex of the upper palea (*Dusén 16057*, SI). —B. *P. malmeanum*, upper palea (*Killeen 2024*, SI). —C. *P. heterotrichon*, upper palea with silica bodies and macrohairs (*Tovar 4176*, US). —D. *P. cordatum*, apex of the upper palea (*Weddell 1699*, P). —E. *P. stellatum*, spikelet base, ventral view (*Killeen 2474*, SI). —F. *P. heterotrichon*, spikelet base, ventral view (*Tovar 4176*, US).

Inflorescences. Inflorescences are usually terminal; axillary inflorescences are common in *Paspalum buchtienii* and *P. polyphyllum.* The number of racemes varies from a single one, e.g., *P. stellatum* and *P. carinatum,* to two conjugate racemes, e.g., *P. malmeanum, P. eucomum, P. reticulinerve,* and *P. pectinatum,* while two alternate racemes are characteristic of *P. goyasense.* When several racemes are present, these can be alternate and distant, e.g., *P. trachycoleon, P. heterotrichon, P. ceresia, P. imbricatum, P. humboldtianum, P. polyphyllum, P. cymbiforme, P. aspidiotes,* and *P. niquelandiae,* or they can be subdigitate (with a short internode, up to 1 cm long, between the racemes) as in *P. cordatum, P. lanciflorum,* and *P. cachimboense.* Pulvini are pilose, and one or two bracts are usually present in *P. stellatum, P. eucomum, P. goyasense, P. malmeanum, P. carinatum,* and *P. pectinatum.*

Rachis of the racemes. Species of *Paspalum* subg. *Ceresia* are typically distinguished by a winged, membranous to foliaceous rachis, 0.8–10 mm wide; the rachis is usually glabrous, occasionally pilose (in *Paspalum polyphyllum*) or ciliate at the margins (in *P. reticulinerve*); hyaline to membranous, and nerveless margins are present in several species, e.g., *P. lanciflorum, P. cachimboense, P. imbricatum, P. pectinatum, P. aspidiotes, P. heterotrichon, P. cymbiforme, P. ceresia, P. stellatum, P. eucomum, P. malmeanum, P. carinatum, P. goyasense, P. biaristatum,* and *P. longiaristatum.*

Although the rachis usually ends in a naked point, in several species, such as *P. humboldtianum, P. buchtienii, P. polyphyllum, P. niquelandiae,* and *P. burmanii,* the rachis finishes in a naked point or in a spikelet; in *P. goyasense* the rachis always ends in a developed spikelet. Spikelets are imbricate and arranged in two or four series.

Spikelets. Spikelets are solitary or paired, dorsiventrally compressed, ranging from ovoid to ellipsoid to lanceolate. The size of spikelets varies from 1.4 to 8 mm in length; they are usually covered with indument, otherwise ciliate; glabrous spikelets are found in *Paspalum phyllorhachis* and *P. imbricatum.* Awned bracts are present only in *P. longiaristatum* and *P. biaristatum.* The lower glume is always absent, while the upper glume is usually as long as the spikelet and 3- to 5-nerved, 7(–9)-nerved in *P. aspidiotes* and *P. reticulinerve,* occasionally 2-nerved in *P. stellatum.* Also, the upper glume is cordate and winged in *P. imbricatum, P. reticulinerve, P. aspidiotes, P. cordatum,* and *P. pectinatum.* The lower lemma is winged in *P. imbricatum, P. reticulinerve,* and *P. aspidiotes.* A lower palea and lower flower are always absent.

Upper anthecium (Figs. 1, 2). The upper anthecium is planoconvex, ellipsoid, ovoid or obovoid, usually hyaline to membranous, but membranous to chartaceous in *Paspalum niquelandiae* and *P. goyasense.* Margins of the upper lemma are flat, not enclosing the apex of the upper palea. A short stipe is present in *P. stellatum, P. lanciflorum, P. cachimboense,* and *P. aspidiotes.*

Regarding the upper anthecium ornamentation, simple papillae regularly distributed, bicellular microhairs and macrohairs, more densely placed toward the apex of the upper lemma and palea, are common features of most species in subgenus *Ceresia.* A smooth and glabrous upper anthecium is present in *Paspalum malmeanum, P. eucomum,* and *P. stellatum.* Bicellular microhairs, 50–70 μm long, have a short basal cell and an elongated apical cell. Unicellular macrohairs, present or absent in subgenus *Ceresia,* can be short and hooked, ca. 40 μm long, to long and thin, 60–300 μm long. Rounded or elongated silica bodies are frequent in several species; these silica bodies have usually 2 to 4 constrictions; 6 or more invaginations are present in *P. lanciflorum.*

DISTRIBUTION AND HABITAT

Species of *Paspalum* subg. *Ceresia* grow in America, ranging from Mexico, Mesoamerica, and the Caribbean (Haiti, the Dominican Republic, and Trinidad and Tobago), to South America (Colombia, Venezuela, Guyana, Surinam, Brazil, Ecuador, Peru, Bolivia, Paraguay, central Argentina, and Uruguay). Brazil hosts the largest number of species, 22, and endemics, 10, in the subgenus.

Taxa are usually found in limestone, sandy, or rocky soils, in open fields or mountain slopes, from sea level to 3000 m elevation. Several species, such as *P. carinatum, P. lanciflorum,* and *P. pectinatum,* are found in open areas subjected to periodic fires; these species have culms and sheaths adapted to fire. *Paspalum malmeanum* and *P. cordatum* grow in flooded savannas.

Paspalum stellatum, P. pectinatum, and *P. carinatum* are the most widespread species in subgenus *Ceresia. Paspalum stellatum* grows from Mexico to southern Brazil, Paraguay, northeastern Argentina, and Uruguay; *Paspalum pectinatum* is found from Mexico to southern Brazil, and *P. carinatum* from Nicaragua to Brazil and Trinidad and Tobago. Regarding the biogeographical distribution of subgenus *Ceresia,* species are common in cerrados, Atlantic forests, and savannas; they are also present in caatingas of northeastern Brazil and in the Guyana highlands of Guyana and Venezuela; they are

Table 3. List of synapomorphies of the cladogram shown in Figure 4, with character state changes in the 37 nodes and within taxa. Characters in bold are common synapomorphies for all 40 most parsimonious trees.

Nodes 1–37

Node 1: character **55**: 0 ⇒ 1, character **57**: 0 ⇒ 1
Node 2: character 54: 0 ⇒ 1
Node 3: character **7**: 0 ⇒ 1, character **14**: 0 ⇒ 1, character **17**: 0 ⇒ 1, character **34**: 0 ⇒ 1
Node 4: character **11**: 0 ⇒ 1, character **27**: 2 ⇒ 1, character 28: 1 ⇒ 0, character 43: 2 ⇒ 1
Node 5: character 40: 0 ⇒ 1, character **51**: 2 ⇒ 1, character **52**: 0 ⇒ 1, character 56: 0 ⇒ 1
Node 6: character **9**: 3 ⇒ 2
Node 7: character **24**: 0 ⇒ 1, character **26**: 0 ⇒ 2, character **30**: 1 ⇒ 2
Node 8: character **26**: 0 ⇒ 1, character **50**: 0 ⇒ 1
Node 9: character **19**: 0 ⇒ 1, character **20**: 0 ⇒ 1, character **27**: 1 ⇒ 2, character **30**: 1 ⇒ 0, character **31**: 0 ⇒ 1
Node 10: character **42**: 0 ⇒ 1
Node 11: character **36**: 0 ⇒ 1, character **40**: 1 ⇒ 0
Node 12: character **23**: 0 ⇒ 1, character **27**: 2 ⇒ 3, character **32**: 0 ⇒ 1, character **39**: 0 ⇒ 1
Node 13: character **42**: 0 ⇒ 1, character **55**: 0 ⇒ 1
Node 14: character **4**: 0 ⇒ 1
Node 15: character **46**: 1 ⇒ 0, character **54**: 1 ⇒ 0
Node 16: character 49: 0 ⇒ 1, character 56: 1 ⇒ 0, character 57: 1 ⇒ 0
Node 17: character 26: 2 ⇒ 1, character 29: 1 ⇒ 0, character 30: 2 ⇒ 3
Node 18: character 45: 1 ⇒ 0, character 46: 0 ⇒ 3
Node 19: character 18: 1 ⇒ 0, character **21**: 0 ⇒ 1, character **38**: 0 ⇒ 1, character 48: 0 ⇒ 1
Node 20: character **18**: 1 ⇒ 0
Node 21: character 13: 0 ⇒ 1, character 16: 0 ⇒ 1
Node 22: character 10: 3 ⇒ 2
Node 23: character 40: 1 ⇒ 0, character **53**: 1 ⇒ 0, character **55**: 1 ⇒ 0
Node 24: character **22**: 0 ⇒ 1, character 40: 1 ⇒ 0
Node 25: character **11**: 1 ⇒ 2, character **25**: 0 ⇒ 1
Node 26: character **33**: 0 ⇒ 1
Node 27: character **53**: 1 ⇒ 0
Node 28: character **15**: 2 ⇒ 1, character **18**: 0 ⇒ 1
Node 29: character **1**: 0 ⇒ 1, character **12**: 0 ⇒ 1
Node 30: character 57: 1 ⇒ 0
Node 31: character 28: 0 ⇒ 1, character 44: 0 ⇒ 1
Node 32: character 9: 3 ⇒ 2, character **30**: 1 ⇒ 2, character **46**: 1 ⇒ 2
Node 33: character 55: 1 ⇒ 0
Node 34: character 10: 0 ⇒ 1
Node 35: character **2**: 0 ⇒ 1, character **3**: 0 ⇒ 1
Node 36: character 24: 0 ⇒ 1, character 26: 0 ⇒ 3, character 40: 0 ⇒ 1, character 42: 0 ⇒ 1
Node 37: character 43: 2 ⇒ 1, character 44: 1 ⇒ 0

Outgroup taxa

Panicum obtusum: character **6**: 1 ⇒ 0, character **27**: 2 ⇒ 3
Anthaenantiopsis fiebrigii: character 24: 0 ⇒ 1, character 26: 0 ⇒ 3, character **30**: 1 ⇒ 0, character 40: 0 ⇒ 1, character 42: 0 ⇒ 1, character 51: 2 ⇒ 1, character **52**: 0 ⇒ 1
Paspalum cromyorrhizon: character **4**: 0 ⇒ 1
P. notatum: no autapomorphies
P. almum: character 10: 0 ⇒ 1, character **57**: 1 ⇒ 0
P. acuminatum: character **30**: 1 ⇒ 0, character **35**: 1 ⇒ 0, character **46**: 1 ⇒ 0, character **56**: 0 ⇒ 1
P. dissectum: character 10: 1 ⇒ 2, character **49**: 0 ⇒ 1, character **57**: 1 ⇒ 0
P. sanguinolentum: character **15**: 0 ⇒ 2
P. erianthum: character 15: 0 ⇒ 1, character **18**: 1 ⇒ 0, character **35**: 1 ⇒ 0, character **55**: 1 ⇒ 0
P. guttatum: character **4**: 0 ⇒ 1, character **46**: 1 ⇒ 0, character **54**: 1 ⇒ 2
P. prostatum: character **55**: 1 ⇒ 0
P. candidum: character **35**: 1 ⇒ 0, character **46**: 1 ⇒ 0
P. racemosum: character **54**: 1 ⇒ 0

Ingroup taxa: Subg. *Ceresia*

P. lanciflorum: character **56**: 1 ⇒ 0
P. cachimboense: character **1**: 0 ⇒ 1, character **55**: 1 ⇒ 0
P. pectinatum: no autapomorphies
P. cordatum: character **4**: 0 ⇒ 1, character **10**: 3 ⇒ 1
P. imbricatum: character **5**: 0 ⇒ 2
P. reticulinerve: character **10**: 3 ⇒ 1, character **15**: 0 ⇒ 1
P. aspidiotes: character **9**: 2 ⇒ 3, character **50**: 0 ⇒ 1
P. goyasense: character **11**: 1 ⇒ 0, character **57**: 1 ⇒ 0
P. carinatum: character 48: 0 ⇒ 1
P. eucomum: character 48: 0 ⇒ 1
P. malmeanum: character **53**: 1 ⇒ 0
P. ceresia: character **35**: 1 ⇒ 0, character **51**: 1 ⇒ 0, character **53**: 1 ⇒ 0, character 55: 0 ⇒ 1
P. stellatum: character 49: 0 ⇒ 1, character **50**: 0 ⇒ 1, character 56: 1 ⇒ 0, character 57: 1 ⇒ 0
P. longiaristatum: character **1**: 0 ⇒ 1, character 55: 0 ⇒ 1
P. biaristatum: no autapomorphies
P. heterotrichon: character **26**: 2 ⇒ 1, character **54**: 1 ⇒ 0
P. petrense: character **42**: 0 ⇒ 1
P. trachycoleon: no autapomorphies
P. phyllorhachis: character **24**: 1 ⇒ 0, character **26**: 2 ⇒ 0, character **46**: 1 ⇒ 2
P. cymbiforme: no autapomorphies
P. buchtienii: no autapomorphies
P. humboldtianum: character **26**: 2 ⇒ 3
P. polyphyllum: character **26**: 2 ⇒ 3, character **40**: 0 ⇒ 1, character **42**: 0 ⇒ 1
P. niquelandiae: character **26**: 2 ⇒ 0, character **55**: 1 ⇒ 0, character **56**: 1 ⇒ 0

less frequent in the Amazonian forests. Several species have an Andean distribution: *P. humboldtianum*, from Mexico and Mesoamerica to northwestern and central Argentina; *P. buchtienii* is restricted to mountain slopes of Bolivia and Peru, while *P. cymbiforme* is found in Mexico and Mesoamerica. A disjunct distribution was observed in the following species: *P. polyphyllum*, present in southern and central Brazil, in the states of Rio Grande do Sul and Santa Catarina, southern Paraguay, northeastern Argentina, and Uruguay, and also in Colombia

Table 4. List of species of informal groups of *Paspalum* Eriantha, Dissecta, Notata, and Racemosa used as outgroups in the cladistic analysis and species of *Paspalum* subg. *Ceresia* and its sections *Ceresia* and *Pectinata*.

Outgroups		
Dissecta Group (sensu Morrone et al., 1996)	*Paspalum acuminatum*	
	P. dissectum	
Eriantha Group (sensu Chase. Ined.)	*P. erianthum*	
	P. guttatum	
	P. sanguinolentum	
Notata Group (sensu Canto-Dorow et al., 1996)	*P. almum*	
	P. cromyorrhizon	
	P. notatum	
Racemosa Group (sensu Morrone et al., 1995)	*P. candidum*	
	P. prostatum	
	P. racemosum	
Paspalum subg. *Ceresia*	section *Pectinata*	*P. aspidiotes*
		P. cachimboense
		P. cordatum
		P. imbricatum
		P. lanciflorum
		P. pectinatum
		P. reticulinerve
	section *Ceresia*	*P. biaristatum*
		P. buchtienii
		P. burmanii
		P. carinatum
		P. ceresia
		P. cymbiforme
		P. eucomum
		P. goyasense
		P. heterotrichon
		P. humboldtianum
		P. longiaristatum
		P. malmeanum
		P. niquelandiae
		P. petrense
		P. phyllorhachis
		P. polyphyllum
		P. stellatum
		P. trachycoleon

and Venezuela. *Paspalum cordatum* has been collected in southern Brazil, Amazonia, and Colombia. *Paspalum ceresia* is common in the Andean region from Ecuador to northwestern Argentina, and isolated populations grow in central Brazil, in the states of Goiás, Maranhão, Minas Gerais, and Pará. Finally, *P. trachycoleon* grows from Mexico and Mesoamerica to Colombia and Venezuela and reappears in southern Brazil.

As previously mentioned, a significant concentration of species is found in the cerrados of central Brazil. *Paspalum biaristatum*, *P. longiaristatum*, *P. burmanii*, and *P. niquelandiae* are restricted to serpentine soils of the state of Goiás; *P. petrense*, *P. imbricatum*, and *P. goyasense* are endemic species of this state; *P. cachimboense* was found only in the Serra do Cachimbo, state of Mato Grosso, on the border with the state of Pará, and *P. phyllorhachis* in Minas Gerais. Another species of subgenus *Ceresia* endemic to central Brazil is *P. eucomum*, present in Minas Gerais, São Paulo, Paraná, Goiás, and in the Distrito Federal. It is noteworthy to mention this high number of endemic species in serpentine soils, characterized by high concentrations of nickel, chromium, cobalt, and other minerals (Brooks, 1987), combined with a low percentage of nutrients in these soils. Other endemic grasses were also previously described for this region (see Filgueiras et al., 1993, for a detailed analysis of the area).

Phylogenetic Analysis

The cladistic analysis using NONA resulted in 40 most parsimonious trees, each of 196 steps, found in 84 of 100 replications, with CI = 38 and RI = 68. Searches to find possible islands yielded no additional trees.

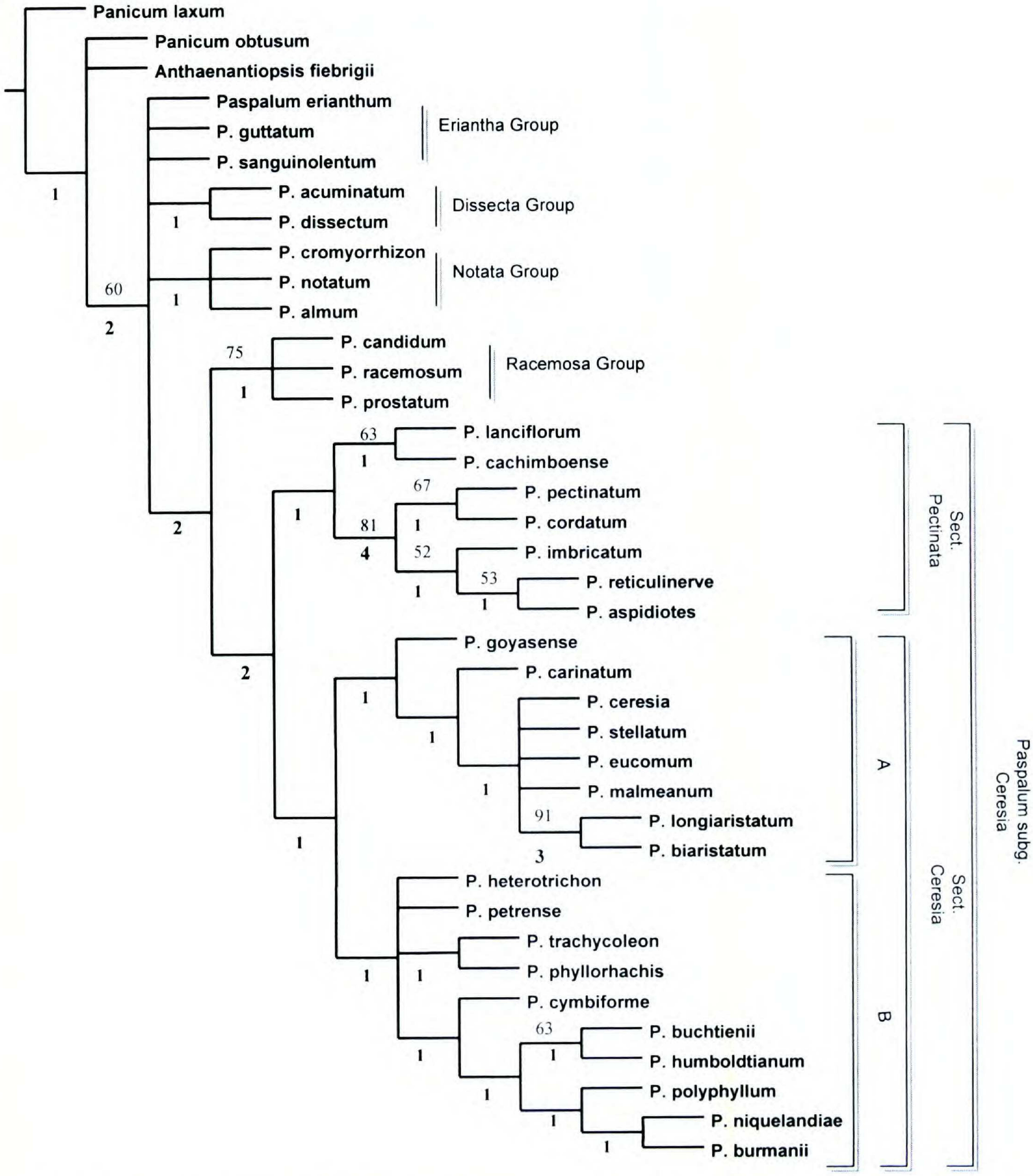

Figure 3. Strict consensus tree from 40 most parsimonious cladograms found by NONA. Numbers below branches indicate Bremer support; numbers above branches indicate jackknife values.

Figure 4 shows one of the 40 most parsimonious trees. Unambiguous synapomorphies of each node are listed in Table 3, which indicates if a character state change occurs just in that cladogram or in all equally parsimonious trees.

The strict consensus is shown in Figure 3, with Bremer support values and jackknife frequencies. In this consensus tree, *Paspalum* is monophyletic with *Anthaenantiopsis fiebrigii* or *Panicum obtusum* as sister taxa. Next within *Paspalum*, there is a major clade including the Racemosa group and subgenus *Ceresia*. Relationships of the remaining studied species of the genus, of Eriantha, Notata, and Dissecta groups, are not solved; they are placed in a basal polytomy in the tree. Two different topologies are equally parsimonious when solving this polytomy, according to the placement of species of the group Eriantha.

The clade comprising groups Racemosa and *Ceresia* (Fig. 4, see node 4) is supported in all most

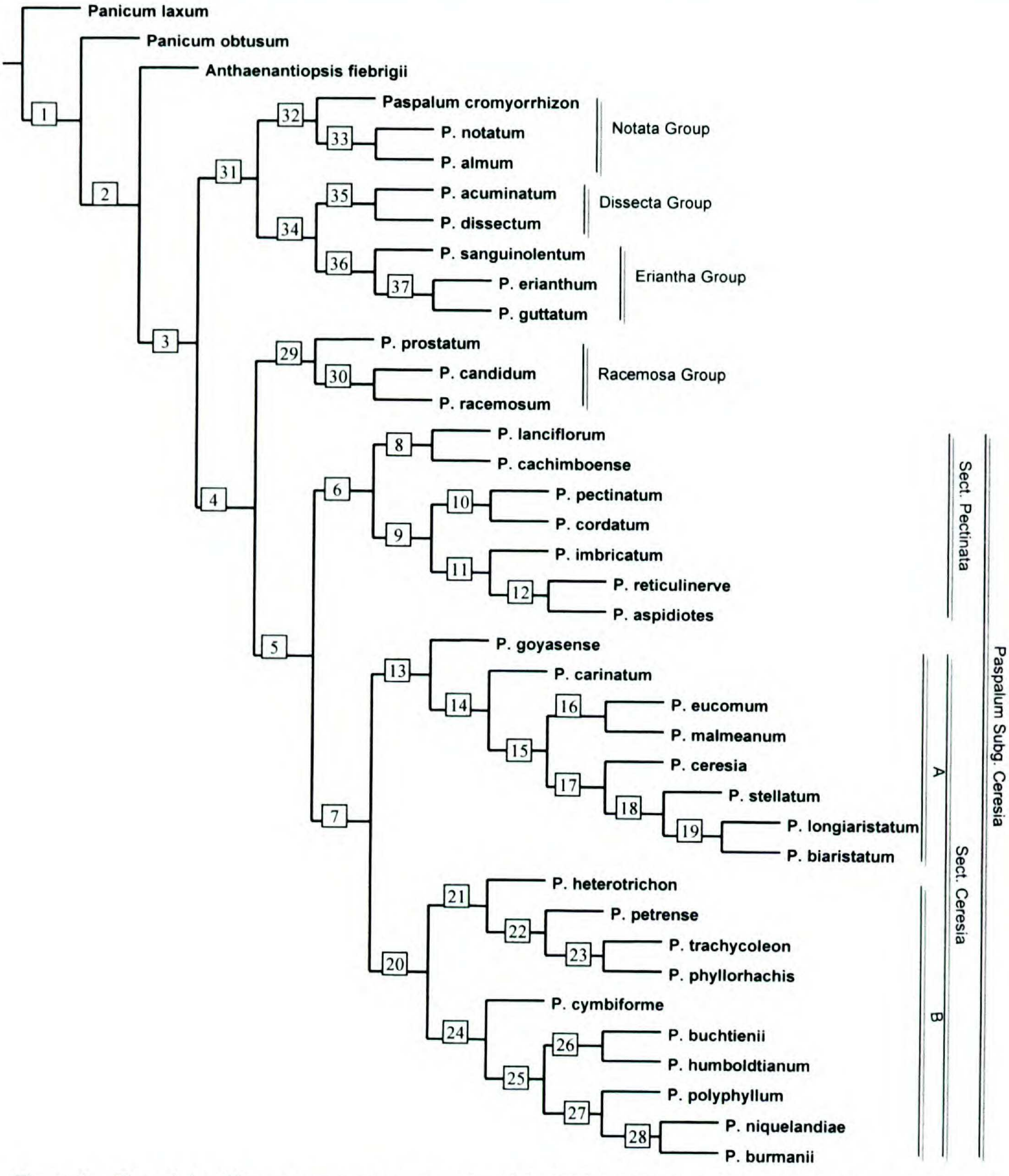

Figure 4. One of the 40 most parsimonious trees found by NONA (196 steps length, CI = 38, RI = 68) with number of nodes in boxes. Synapomorphies of each node and taxa are listed in Table 3.

parsimonious trees by character 11 (apex of the rachis ending in a naked point) and character 27 (upper glume 3-nerved). In some of the most parsimonious trees, character 28 (nerves of the upper glume equidistant) and character 43 (lower lemma 3-nerved) also support this clade.

Paspalum subg. *Ceresia* forms a clade with Racemosa as its sister group. At node 5 (Fig. 4), characters supporting the monophyly of subgenus *Ceresia* are: 51 (membranous upper anthecium) and 52 (upper palea gaping at the apex). Characters 40 (lower lemma with pilose margins) and 56 (upper lemma with unicellular macrohairs) also support subgenus *Ceresia* in some of the most parsimonious trees.

Within *Paspalum* subg. *Ceresia*, two major clades appear in the analysis: one containing species of section *Pectinata*, and the other containing the remaining species of the subgenus. Section *Pectinata* (see node 6, Fig. 4) is supported by character 9

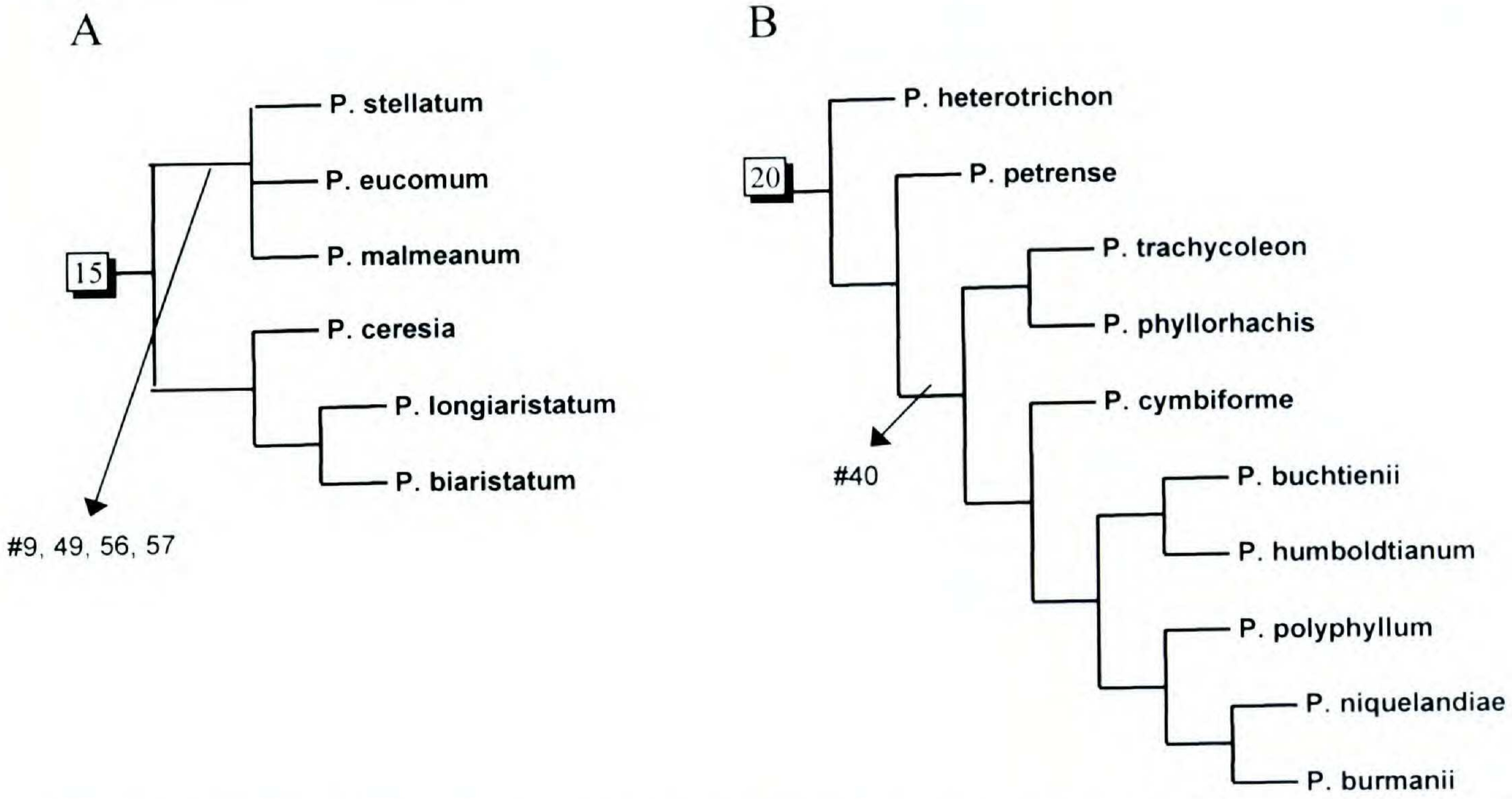

Figure 5. Alternative most parsimonious topologies within *Paspalum* sect. *Ceresia*.—A. Node 15 of cladogram of Figure 4. —B. Node 20 of cladogram of Figure 4.

(presence of approximate racemes); within this section, *P. pectinatum*, *P. cordatum*, *P. imbricatum*, *P. reticulinerve*, and *P. aspidiotes* are grouped together and are very well supported by the presence of characters 19, 20, 27, 30, and 31 (upper glume winged, cordate, 5-nerved, with flat margins, and marginal nerves not reaching the apex) in all of the most parsimonious trees.

The other main clade (see node 7, Fig. 4), including species here considered to be in section *Ceresia*, is supported, in all shortest trees, by characters 24 (upper glume with pilose margins), 26 (upper glume hairy on the lower half), and 30 (margins of the upper glume folded at the nerve). Within this clade, two subgroups (Figs. 3, 4) are recognized: clade A, including *P. goyasense*, *P. carinatum*, *P. eucomum*, *P. malmeanum*, *P. ceresia*, *P. stellatum*, *P. longiaristatum*, and *P. biaristatum*, with the following characters as synapomorphies (node 13, Fig. 4): 42 (lower lemma pilose) and 55 (upper anthecium without silica bodies). In all of the most parsimonious trees, *P. longiaristatum* and *P. biaristatum* constitute a well-supported terminal group (node 19, Fig. 4), both species with an awned upper glume and lower lemma (chars. 21 and 38). Clade B includes *P. heterotrichon*, *P. petrense*, *P. trachycoleon*, *P. phyllorhachis*, *P. cymbiforme*, *P. buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*, and is defined by character 18 (hyaline upper glume) in all trees (node 20, Fig. 4).

Two equally parsimonious topologies were found in clade A: one shown in Figure 4 (node 18), where *P. stellatum* is the sister species of *P. longiaristatum* and *P. biaristatum*, due to support from characters 45 and 46 (lower lemma with marginal nerves and extension of the margins absent). In the other resolution, shown in Figure 5A, *P. stellatum*, *P. eucomum*, and *P. malmeanum* constitute a group supported by characters 9 (two racemes per inflorescence), 49 (obovoid upper anthecium), and 56 and 57 (upper anthecium without macro- and microhairs), with *P. ceresia* as the sister species of *P. longiaristatum* and *P. biaristatum*.

On the other hand, two equally parsimonious topologies were obtained for clade B: in one of them, shown in Figure 4, *P. heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis* are monophyletic (node 21), being sustained by characters 13 (spikelets laterally inserted in the pedicels) and 16 (spikelets with an annular thickening at the base). The alternative topology (Fig. 5B) places *P. trachycoleon* and *P. phyllorhachis* as sister group to a clade consisting of *P. cymbiforme*, *P. buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*. This clade, with eight species, shares a glabrous margin of the lower lemma (char. 40).

Two most parsimonious trees (fit = 413.7 and 199 steps) were obtained using implied weights with PeeWee (trees not included). Regarding the *Paspalum* ingroup, the strict consensus of both trees has the same topology as the tree, obtained with NONA (Fig. 3), where group Racemosa is the sister to subgenus *Ceresia*. Characters supporting clades in the two shortest trees are the same as in the equal weight analysis, except character 24 for section *Ceresia* (node 7, Fig. 4). In both most parsimonious trees from Pee Wee, groups Eriantha, Dissecta, and Notata are more closely related to each other than to the clade group Racemosa + subgenus *Ceresia*.

DISCUSSION

Monophyly of *Paspalum* subg. *Ceresia* is sustained by the present analysis. Two additional steps are required for breaking down the subgenus *Ceresia* clade, which has a Bremer support of 2 and a jackknife value less than 50; similar low values are common in different cladistic treatments using morphological data (Karis, 1995). Only homoplasic characters support this clade including subgenus *Ceresia*: a membranous upper anthecium (char. 51) is present in nearly all species of the ingroup, but *P. niquelandiae* and *P. goyasense* have a membranous or chartaceous upper anthecium, whereas in *P. ceresia* it is hyaline. Regarding the outgroups, the upper anthecium is membranous in *Anthaenantiopsis fiebrigii*, and membranous to chartaceous in *P. candidum* and *P. cromyorrhizon*. Character 52 (upper palea gaping at the apex, not covered by the upper lemma) is a synapomorphy of the subgenus but also present in *A. fiebrigii*. The winged rachis, widely used to recognize the subgenus, is present in many of the outgroup taxa, evidently arising many times, or being lost, in the evolution of the genus.

Within subgenus *Ceresia* two monophyletic sections are recognized: section **Pectinata**, including *Paspalum lanciflorum*, *P. cachimboense*, *P. pectinatum*, *P. cordatum*, *P. imbricatum*, *P. reticulinerve*, and *P. aspidiotes*, and section **Ceresia**, including *P. goyasense*, *P. carinatum*, *P. eucomum*, *P. malmeanum*, *P. ceresia*, *P. stellatum*, *P. longiaristatum*, *P. biaristatum*, *P. heterotrichon*, *P. petrense*, *P. trachycoleon*, *P. phyllorhachis*, *P. cymbiforme*, *P. buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*. Section *Pectinata* is weakly supported herein (Bremer support = 1; jackknife value less than 50); a similar delimitation of section *Pectinata* was recently shown by Rua and Aliscioni (in press). Within this section, the group including *P. pectinatum*, *P. cordatum*, *P. imbricatum*, *P. reticulinerve*, and *P. aspidiotes* is well supported (Bremer support = 4; jackknife value = 81), all species sharing a winged and cordate, 5- or more nerved upper glume, with the marginal nerves not reaching the upper third of the glume. *Paspalum lanciflorum* and *P. cachimboense* are basal species within section *Pectinata*, both taxa without a winged and cordate upper glume, but with a lower lemma pilosity similar to other species of section *Pectinata*.

Section *Ceresia* is also weakly supported herein (Bremer support = 1; jackknife value less than 50). Within the section, *Paspalum biaristatum* and *P. longiaristatum* are well-supported sister species (Bremer support = 3; jackknife value = 91) but are not distinct from section *Ceresia*. Therefore, we consider section *Biaristata* (Filgueiras & Davidse, 1994) as included in section *Ceresia*, because retaining section *Biaristata* within our section *Ceresia* will render section *Ceresia* monophyletic.

TAXONOMIC TREATMENT

Paspalum subg. **Ceresia** (Persoon) Reichenbach, Consp. Regn. Veg.: 49. 1828. *Ceresia* Pers., Syn. Pl. 1: 85. 1805. *Paspalum* sect. *Ceresia* (Pers.) Nees, Fl. Bras. Enum. Pl. 2: 76. 1829, [as "Paspalus sect. Ceresiae"]. *Paspalum* sect. *Ceresia* (Pers.) Schltdl. ex Müll. Stuttg., Bot. Zeitung (Berlin) 19: 326. 1861, nom. illeg. *Paspalum* subsect. *Ceresia* (Pers.) Benth., Gen. Pl. 3: 1098. 1883. *Paspalum* sect. *Ceresia* (Pers.) Pilg., Repert. Spec. Nov. Regni Veg. 26(15): 230. 1929, nom. illeg. TYPE: *Paspalum ceresia* (Kuntze) Chase [= *Ceresia elegans* Pers.].

Paspalum sect. *Biaristata* Filgueiras & Davidse, Novon 4: 20. 1994. Syn. nov. TYPE: *Paspalum biaristatum* Filg. & Davidse.

Paspalum sect. **Pectinata** Chase ex Rodr.-Rodr., Ernstia 2(1–2): 22. 1992. TYPE: *Paspalum pectinatum* Nees ex Trin.

Plants perennial, erect or leaning on the vegetation. Blades rigid, filiform to lanceolate. Inflorescences with 1 to several racemes, rachis of the racemes winged, hyaline to membranous, 0.8–10 mm wide. Spikelets 1.4–8 mm long, pilose, occasionally glabrous; lower glume absent; lower palea and lower flower absent; upper anthecium pale, hyaline to membranous, chartaceous in some species, the palea free at the apex.

Twenty-five species growing from Mexico to Argentina, Uruguay, and southern Brazil.

Cerea Schltdl., Bot. Zeitung (Berlin) 12: 820. 1854, is a superfluous name for *Ceresia*.

KEY TO DISTINGUISH THE SPECIES OF *PASPALUM* SUBG. *CERESIA*

1. Upper glume winged 2
1′. Upper glume not winged 6
2(1). Spikelets glabrous .... 14. *P. imbricatum*
2′. Spikelets pilose 3
3(2). Spikelets paired, arranged in four series .... 23. *P. reticulinerve*
3′. Spikelets solitary, arranged in two series 4
4(3). Lower lemma shortly ciliate on the margins, not papillose-pilose .... 1. *P. aspidiotes*
4′. Lower lemma conspicuously papillose-pilose on the margins 5
5(4). Culms short rhizomatous, 35–100 cm tall; sheaths red or brown, shiny at the outer surface; racemes 2(3 to 5), 2–8 cm long; spike-

lets lanceolate, 5–8 mm long, 2–3.3 mm wide ... 19. *P. pectinatum*

5′. Culms with long, curved rhizomes, 100–130 cm tall; sheaths stramineous or green, not shiny at the outer surface; racemes 5 to 10, 12–16 cm long; spikelets ovoid, 4–5(–6) mm long, 2.5–3.5 mm wide ... 8. *P. cordatum*

6(1). Spikelets with the upper glume and the lower lemma awned ... 7

6′. Spikelets not awned ... 8

7(6). Annual, culms 15–36 cm tall; spikelets 1.8–2.2 mm long; awn of the upper glume 6–12.2 mm long, that of the lower lemma 0.3–2 mm long ... 16. *P. longiaristatum*

7′. Perennial, culms 70–125 cm tall; spikelets 3.8–4.5 mm long; awn of the upper glume 4–7.1 mm long, that of the lower lemma 3.8–4.5 mm long ... 2. *P. biaristatum*

8(6). Rachis (3.5–)4–10 mm wide ... 9

8′. Rachis 1–2.5(–3) mm wide ... 15

9(8). Spikelets solitary ... 10

9′. Spikelets paired ... 13

10(9). Spikelet (4.8–)5.6–7.2 mm long; anthecium ½ to ⅓ length of the spikelet ... 15. *P. lanciflorum*

10′. Spikelet 2.3–3.9 mm long; anthecium as long as or slightly shorter than the spikelet ... 11

11(10). Inflorescences with 1 (rarely 2) racemes, if 2 conjugate; pulvini with 1 or 2 papyraceous bracts; pedicels with a crown of hairs toward the apex; upper anthecium shortly stipitate; blades filiform ... 24. *P. stellatum*

11′. Inflorescences with 1 to 7 alternate racemes; pulvini ebracteate; pedicels hispid, without a crown of hairs toward the apex; upper anthecium not stipitate; blades linear to linear-lanceolate (occasionally filiform in *P. ceresia*) ... 12

12(11). Rachis 3.5–4 mm wide; blades 1.5–4 mm wide; spikelets 2.3–3 mm long, not early deciduous, with an annular thickening at the base; upper glume with papillose-pilose hairs toward the margins, a few of them longer than the rest; lower lemma with long hairs at the upper margins, otherwise glabrous; lodicules 2 ... 12. *P. heterotrichon*

12′. Rachis 6–10 mm wide; blades 3–15(–20) mm wide; spikelets (3–)3.4–3.6 mm long, early deciduous, without an annular thickening at the base; upper glume with ± equal, silky, not papillose-pilose, marginal hairs; lower lemma pilose all over the surface; lodicules absent ... 7. *P. ceresia*

13(9). Plants bambusiform; spikelets glabrous ... 21. *P. phyllorhachis*

13′. Plants herbaceous; spikelets pilose ... 14

14(13). Culms unbranched, 70–90 cm tall; blades 3–6 mm wide; rachis (6.5–)7–7.5 mm wide; upper glume long-acuminate; lower lemma pilose on the lower half, not sulcate ... 20. *P. petrense*

14′. Culms branching, 1–2 m tall; blades 0.5–1.5 cm wide; rachis 4–6 mm wide; upper glume acute to acuminate; lower lemma pilose at the upper portion or glabrous, sulcate ... 25. *P. trachycoleon*

15(8). Annual; upper anthecium long-stipitate ... 5. *P. cachimboense*

15′. Perennial; upper anthecium not stipitate ... 16

16(15). Spikelets solitary; the margins not corky, with hairs up to 3 mm long, appressed or ascendent, irregularly distributed on the margins ... 17

16′. Spikelets paired, occasionally the lower one reduced or aborted; the margins corky, with radiate marginal hairs (ascendent in *P. cymbiforme*) ... 20

17(16). Racemes 2, conjugate; spikelets 1.6–3 mm long, the margins densely pilose on the upper portion, with hairs up to 2 mm long, shortly pilose toward the base; upper anthecium as long as the upper glume and lower lemma ... 18

17′. Racemes 1 to 3, not conjugate; spikelets 3–5 mm long, with long hairs on the basal margins, sparsely and shortly pilose on the upper portion, occasionally glabrous; upper anthecium shorter than the upper glume and lower lemma ... 19

18(17). Spikelets 1.6–2 mm long ... 17. *P. malmeanum*

18′. Spikelets 2.5–3 mm long ... 10. *P. eucomum*

19(17). Racemes 1, occasionally 2; rachis of the branches 1.8–2.5(–3.5) mm wide, straight to subfalcate; upper glume densely pilose on the lower third, otherwise scaberulous; upper glume and lower lemma flat in the upper portion; blades filiform ... 6. *P. carinatum*

19′. Racemes (1)2(3), rachis of the branches 1–1.6 mm wide, straight; lower glume densely pilose in the lower half, otherwise glabrous; upper glume and lower lemma slightly convex; blades linear ... 11. *P. goyasense*

20. Rachis of the branches 2–3 mm wide ... 21

20′. Rachis of the branches 0.8–1.5(–1.8) mm wide ... 22

21(20). Inflorescences 8–12 cm long, with 1 to 4 racemes; floriferous culms 60–90 cm tall; blades linear, 5–19(–24) × 0.2–0.5(–0.8) cm; pseudoligule a ring of hairs ... 9. *P. cymbiforme*

21′. Inflorescences 20–25 cm long, with 9 to 11 racemes; floriferous culms 150 cm tall; blades lanceolate, 30–35 × 1–1.2 cm; pseudoligule absent ... 4. *P. burmanii*

22(20). Plants robust, 120–185 cm tall, blades 20–45 × 0.8–2.2 cm, inflorescences with 8 to 30 racemes ... 18. *P. niquelandiae*

22′. Plants herbaceous, 30–100 cm tall; blades 4–21 cm long, 0.1–1.8 cm wide, inflorescences with 1 to 11 racemes ... 23

23(22). Rachis pilose on one or both surfaces; blades linear to linear-lanceolate, 4–13 cm long, 0.1–0.6 cm wide; upper glume with unequal marginal hairs; lower lemma with ciliate apical margins ... 22. *P. polyphyllum*

23′. Rachis glabrous; blades lanceolate, 5–21 cm long, 0.5–1.8 cm wide; upper glume with marginal hairs evenly distributed, all of the same length; lower lemma with glabrous apical margins ... 24

24(23). Racemes (4)7 to 11, arcuate; rachis of the branches 0.8–1.2(–1.4) mm wide; spikelets 0.8–1(–1.3) mm wide, sparsely distributed; blades papyraceous ... 3. *P. buchtienii*

24′. Racemes 2 to 6, not arcuate; rachis of the branches 1.2–1.5 mm wide; spikelets 1.2–1.4 mm wide, imbricate; blades herbaceous .... 13. *P. humboldtianum*

1. **Paspalum aspidiotes** Trinius, Sp. Gram. 3: pl. 269. 1829–1830. TYPE: Brazil. Without locality: *G. H. von Langsdorff s.n.* (holotype, LE! photo, SI!; isotypes, P!, US-2942148!). Figures 6, 7.

Paspalum setiglume Chase, Brittonia 3: 150, fig. 1. 1939. Syn. nov. TYPE: Venezuela. Bolívar: Auyan-tepuí, 1100 m, Dic. 1937–Jan. 1938, *G. H. H. Tate 1285* (holotype, NY not seen, photo, K!; isotypes, MO-2704419!, US-1723623! photo, SI!).

Paspalum erectifolium Swallen, Fieldiana, Bot. 28: 22. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, bordering forest of Río Karuai, between Santa Teresita de Kavanayén and base of Ptari-tepuí, 1220 m, 18 Nov. 1944, *J. A. Steyermark 60302* (holotype, US-1911668! photo, SI!; isotypes, MO-3001316!, NY not seen, VEN not seen).

Rhizomatous perennial, with arcuate rhizomes; floriferous culms 30–90 cm tall, 0.3–0.4 cm diam., erect, simple or branched; internodes cylindrical, glabrous, finely striate; nodes compressed, shortly pilose, brown. Sheaths usually longer than the internodes, overlapping, densely villous all over the surface or only at the distal portion, the margins pilose. Ligules membranous, 3–4 mm long, ferruginous, glabrous; pseudoligule a tuft of long white hairs. Blades lanceolate, 8–32 cm long, 0.7–1.5 cm wide, attenuate at the base, the apex acuminate, rigid, ascendent, densely villous on both surfaces, the margins pilose. Terminal inflorescence exserted, subdigitate. Peduncles up to 30 cm long, terete, finely striate, glabrous; main axis up to 4 cm long, flattened, glabrous or sparsely pilose; pulvini pilose; racemes 4 to 7, rarely 3, ascendent, 6–13.5 cm long, alternate; rachis of the racemes flattened, 3–4.5 mm wide, ending in a naked point, shortly pilose, the midnerve manifest, the margins membranous, pale to brown; pedicels short, flat, pilose toward the apex; spikelets solitary, densely imbricate in 2 series. Spikelets broadly ovoid, 6.5–7.5 mm long, 3–4 mm wide, dorsiventrally compressed, pilose, ferruginous, upper glume and lower lemma winged, cordate, the apex rounded. Upper glume papyraceous, 7(–9)-nerved, with 3 central nerves reaching the apex and anastomosed veins between the nerves, with 1 to several white hairs, up to 2.5 mm long, at the apex, the rest of the surface short ciliate, the margins ciliate. Lower lemma glumiform, 5.5 mm long, 3.1 mm wide, papyraceous, 5–7-nerved, corrugate toward the basal portion, ciliate, with one to several white hairs, at the upper margins, otherwise scabrous. Upper anthecium long-ellipsoid, 5 mm long, 1.3 mm wide, shorter than the spikelet, membranous, stramineous, plano-convex, shortly stipitate, minutely papillose, with simple papillae all over the surface, scabrous and with a tuft of macrohairs, bicellular microhairs, and silica bodies at the apex; lodicules 2, conduplicate, hyaline, 0.4 mm long; stamens 3, anthers 1.6 mm long; stigmas 2, plumose, lateral. Caryopsis not seen.

Distribution and habitat. *Paspalum aspidiotes* grows in savannas, on dry and rocky soils, between 100 and 1200 m elevation in Venezuela (Amazonas and Bolívar), Colombia (cited by Judziewicz, 1990), Guyana, Brazil (Amazonas), and Bolivia, where it was recently found in Santa Cruz.

Paspalum aspidiotes is related, within section *Pectinata*, to *P. reticulinerve*, the latter distinguished by paired spikelets. It is also related to *P. cordatum* Hack., a species with spikelets 4–5(–6) mm long, without white hairs on the apex of the upper glume and lower lemma, the upper glume and lower lemma not scabrous over the whole surface, and with conspicuous marginal, tuberculate hairs at the lower lemma.

The study of type material of *P. aspidiotes*, from LE, and that of *P. setiglume*, from K, MO, and US, allowed us to verify that there are no differences between the taxa. There is, within the examined specimens, variation in the number and length of the hairs on the upper margins of the upper glume and lower lemma. Therefore, *Paspalum setiglume* is considered a synonym of *P. aspidiotes*.

The specimen *Riedel s.n.*, collected in Brazil without a definite locality and examined at P, probably represents an isotype of *P. aspidiotes* (see Renvoize, 1978, for comments on *Langsdorff* and *Riedel* collections).

Representative specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff M., *Mostacedo et al. 1862* (LPB). BRAZIL. **Amazonas:** Estrada do Estanho, road to Igarapé Preto, *Calderón et al. 2760* (US); Fortaleza Savanna, Rio Puciari tributary of Rio Ituxi, *Prance et al. 13823* (R, US); Mun. Humaitá, estrada Humaitá–Jacarecanga, km 62, *Texeira et al. 1197* (MO). **Without state:** without locality, *Riedel 1048* (B), *Riedel s.n.* (G, P). GUYANA. Imbaimadai savanna, Upper Mazaruni River, Ayanganna Plateaú, *Fraser 370* (US). VENEZUELA. **Amazonas:** Territorio Federal Amazonas, *Guánchez & Melgueiro 3618* (MO). **Bolívar:** La Gran Sabana, km 145 along hwy., *Davidse 4708* (K, MO, US); Distr. Piar, at top of Salto Aicha near E base of Uaipan-tepui, *Davidse & Huber 22944* (MO); Dist. Roscio, S de Cantarana, *Huber & Alarcón 9643* (MO); Distr. Piar, en las cabeceras nororientales del Río Urimán, *Huber et al. 9898* (MO, US); by first ford W along summit Torom-Meru NW of Parupa, *Kral 72050* (MO).

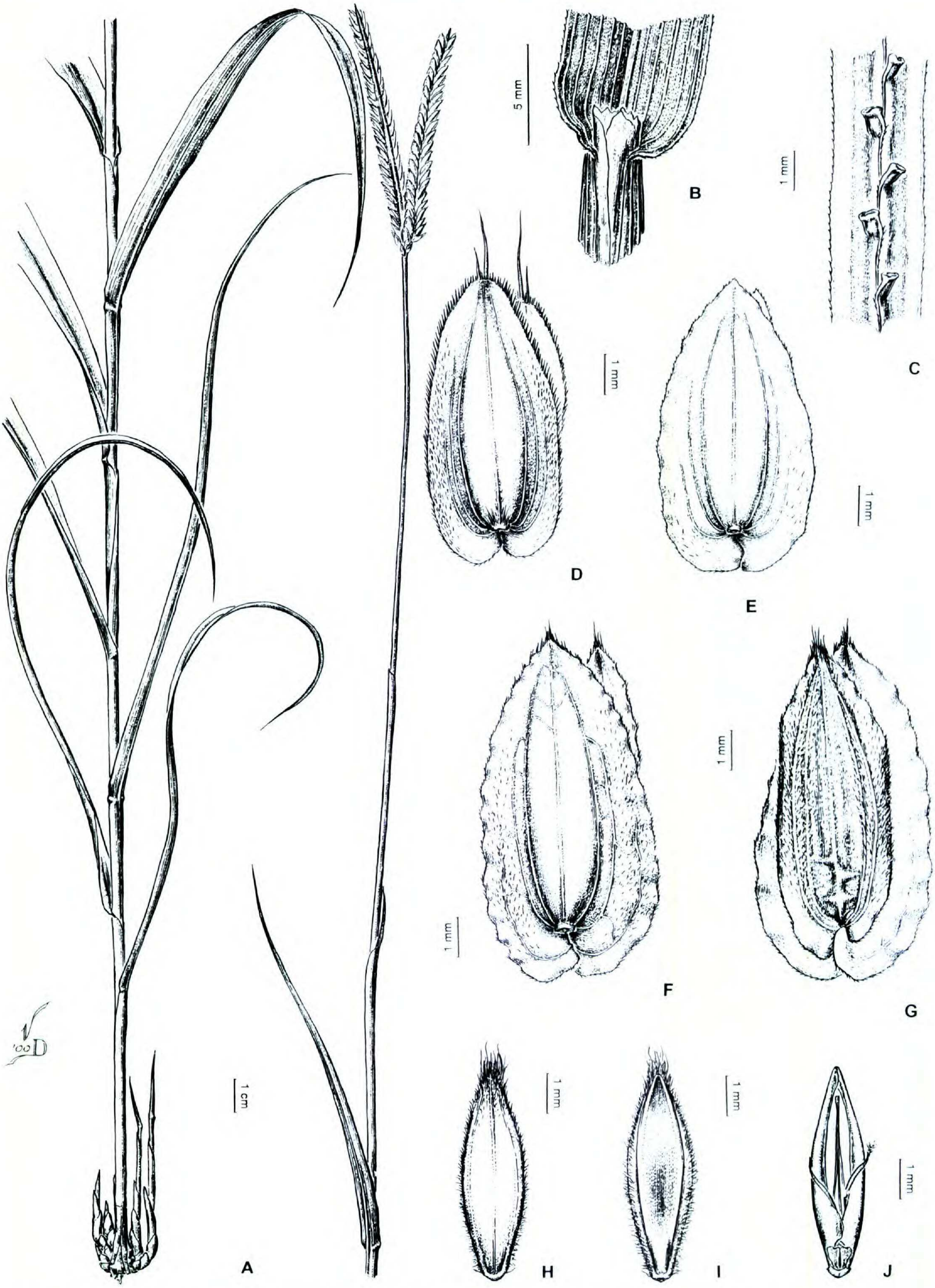

Figure 6. *Paspalum aspidiotes.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D, E, F. Spikelets, upper glume view. —G. Spikelet, lower lemma view. —H. Upper anthecium, dorsal view. —I. Upper anthecium, ventral view. —J. Upper palea, lodicules, and gynoecium. (A–C, E–J based on *Riedel s.n.*, P; D based on *Tate 1285*, US.)

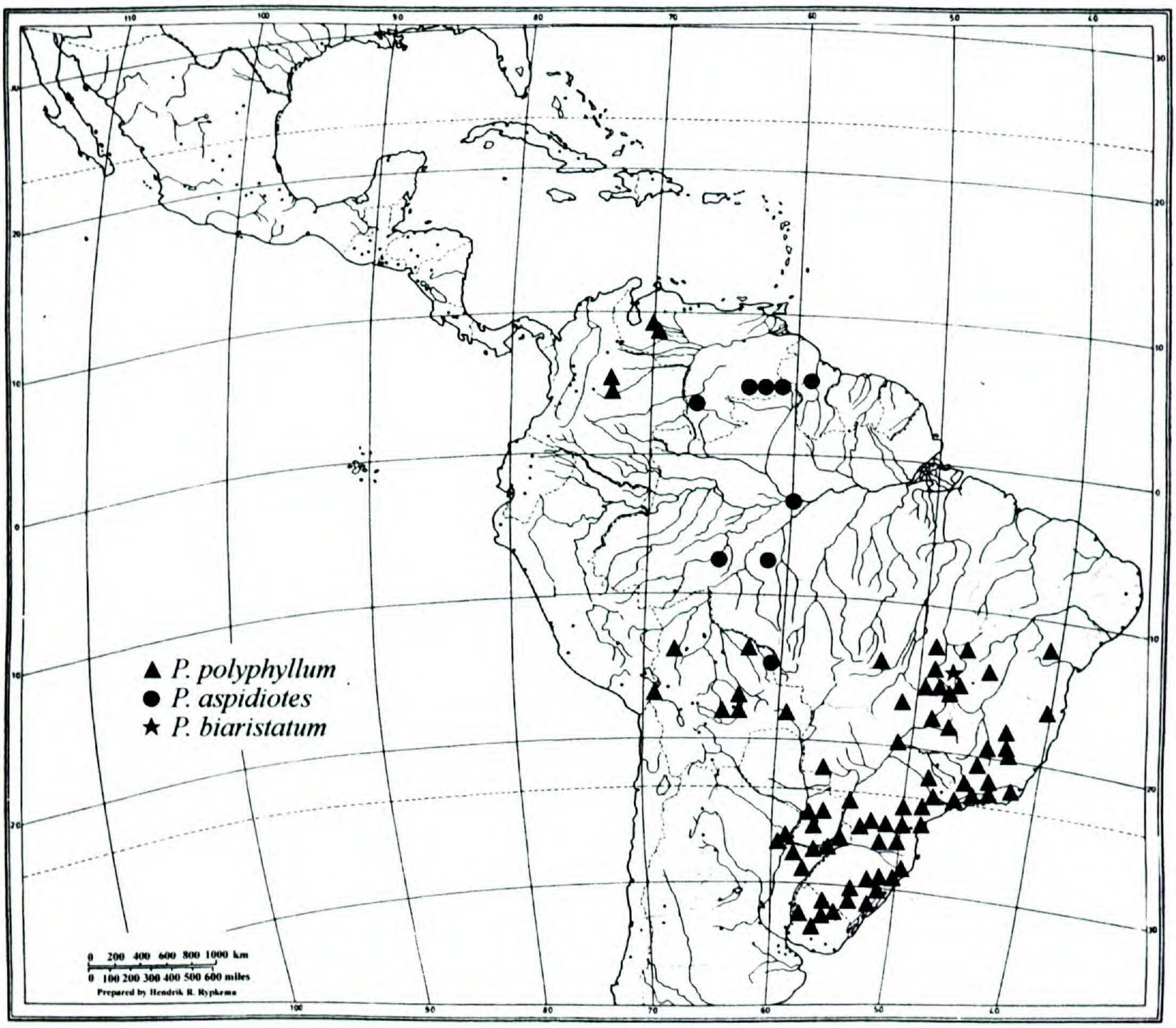
▲ P. polyphyllum
● P. aspidiotes
★ P. biaristatum
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 7. Distribution of *Paspalum aspidiotes*, *P. biaristatum*, and *P. polyphyllum*.

2. **Paspalum biaristatum** Filgueiras & Davidse, Novon 4: 18, fig. 1. 1994. TYPE: Brazil. Goiás: Niquelândia, Macedo, ca. 14°18′S, 48°23′W, 18 km N de Niquelândia, 10 June 1992, *T. S. Filgueiras 2341* (holotype, IBGE!; isotypes, B not seen, F not seen, FLAS not seen, ICN!, ISC not seen, K! photo, SI!, MEXU not seen, MO!, P not seen, R not seen, RB not seen, SI!, SP not seen, UB not seen, US!). Figure 7.

Caespitose, shortly rhizomatous perennial; culms simple or branched, 70–125 cm tall, 1–1.3 mm diam., rigid; internodes cylindrical, hollow, glabrous; nodes dark, the basal ones glabrous or pilose, the upper ones glabrous. Sheaths 4–7 cm long, shorter than the internodes, keeled, with papillose-pilose hairs, the margins glabrous or ciliate. Ligules membranous-ciliate, the membranous portion 0.2–0.3 mm long, cilia 0.2–0.3 mm long; pseudoligule a ring of hairs 1–1.2 mm long. Blades linear to linear-lanceolate, 7–19 cm long, 0.1–0.9 cm wide, papillose-pilose on both surfaces, attenuated or rounded at the base, the apex long-acuminate, the margins ciliate. Peduncles subexserted or exserted, up to 17 cm long, terete. Terminal inflorescences 6–11 cm long, 3–4 cm wide; main axis absent or up to 6 cm long, glabrous, scabrous; racemes 1 to 4(7), 3–8(–13) cm long, solitary or alternate, distant, arcuate, ending in a naked, acuminate point; pulvini pilose; rachis of the racemes 4.5–7 mm wide, glabrous, with a midnerve prominent and margins membranous, sparsely ciliate; pedicels 0.3–0.5 mm long, solitary, hispidulous; spikelets densely imbricate in two series along the rachis. Spikelets long ellipsoid, awned, 3.8–4.5 mm long without the awn, 0.4–0.5 mm wide, pilose, stramineous to purple. Upper glume hyaline, 3-nerved, densely pilose toward the base, with hairs reaching ½–⅓ the length of the spikelet, otherwise glabrous, the margins densely pilose with hairs 1.7–2.2 mm long; awn 4–7.1 mm long, scabrous. Lower lemma slightly shorter than the upper glume, membranous, 3-nerved; terminal awn 3.8–4.5 mm long, scabrous. Upper anthecium ellipsoid, 3–3.5 mm long, 0.5 mm wide, shorter than the spikelet, papyraceous, shiny, pilose on the upper portion; upper lemma 5-nerved, the nerves inconspicuous, with bicellular microhairs and macrohairs toward the apex, the margins hairy on the upper third or glabrous, flattened; upper palea with microhairs, macrohairs, hooks, and silica bodies on the distal portion; lodicules absent; stamens 3, anthers 2–2.2 mm long; stigma plumose. Caryopsis 1.2–1.5 mm long, 0.3–0.5 mm wide; hilum punctiform, embryo less than half the length of the caryopsis.

Distribution and habitat. Endemic to central Brazil; it grows in Niquelândia, Goiás, in serpentine soils at 1000 m.

Paspalum biaristatum is related to *P. longiaristatum* by the presence of awned spikelets. The latter is distinguished by its annual habit, spikelets 1.8–2.2 mm long, upper glume with an awn 6–12.2 mm long, and lower lemma with awn 0.3–2 mm long.

Representative specimens. BRAZIL. **Goiás:** Niquelândia, Mun. Niquelândia, Macedo, *Filgueiras & Lopes 2408, 2409* (MO), *Fonseca et al. 224* (MO), *Oliveira et al. 615, 623, 630* (K), *758* (IBGE, SI).

3. Paspalum buchtienii Hackel, Repert. Spec. Nov. Regni Veg. 6: 153. 1908. TYPE: Bolivia. La Paz: Prov. Sud Yungas, Sirupaya a Yanacachi, 2100 m, 1906, *O. Buchtien 420* (holotype, W! photo, K!; isotype, US-2854141! photo, SI!). Figures 8, 9.

Rhizomatous perennial, with leafy, long rhizomes; floriferous culms 60–100 cm tall, ascendent, erect or clambering, rigid, branching at the basal and middle nodes; internodes 5–25 cm long, 0.2–0.3 cm diam., finely striate, glabrous, hollow, stramineous or tinged with purple; nodes compressed, brown, glabrous to shortly pilose. Sheaths 4–15 cm long, the lower ones overlapping, the upper ones shorter than the internodes, glabrous or pilose, the margins membranous, glabrous or ciliate with tuberculate hairs. Ligules membranous, 0.8–1.6 mm long, brown, glabrous; pseudoligule absent. Blades lanceolate, 6–16 cm long, 0.6–1.7 cm wide, flattened, papyraceous, acute at the apex, glabrous to shortly pilose on both surfaces, the margins glabrous or ciliate, shortly pseudopetiolate, pseudopetiole ciliate. Peduncles up to 28 cm long, terete, glabrous. Terminal and axillary inflorescences present, exserted, 10–15 cm long, 6–9 cm wide, truncate; main axis 4–13 cm long, flattened, glabrous; racemes (4)7 to 11, alternate to subopposite, arcuate, the basal ones 6–12 cm long, rachis of the racemes flattened, 0.8–1.2(–1.4) mm wide, keeled and with longitudinal nerves, green to purple, glabrous, the margins scaberulous, ending in a spikelet or in a naked point; pedicels paired, flattened to triquetrous, glabrous, unequal, the upper up to 0.8 mm long; spikelets paired, occasionally the lower one aborted, sparsely arranged in 2 to 4 series. Spikelets long-ellipsoid, 3–3.6 mm long, 0.8–1(–1.3) mm wide, dorsiventrally compressed, acuminate, pilose, pale or tinged with purple. Upper glume hyaline to membranous, 3-nerved, the margins corky, papillose-pilose with radiate, white hairs, otherwise sparsely pilose. Lower lemma glumiform, membranous, 3-nerved, glabrous or shortly and sparsely pilose on the surface, scabrous, with a depression at the base of the dorsal surface. Upper anthecium long-ellipsoid, 2.2–2.6 mm long, 0.8 mm wide, shorter than the spikelet, plano-convex, membranous, stramineous, finely papillose with simple papillae over the surface, scaberulous toward the apex; upper lemma 5-nerved, the margins flat and not covering the apex of the palea, with silica bodies, microhairs, and hooks at the apex; upper palea with microhairs at the apex; lodicules 2, conduplicate, 0.3 mm long; stamens 3, anthers 1.6 mm long; stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. Paspalum buchtienii grows in Bolivia (La Paz and Santa Cruz) and Peru (see observations), where it is found on mountain slopes on rocky or limestone soils along forest edges from 460 to 2100 m.

Paspalum buchtienii is closely related to *P. humboldtianum*, a species that is distinguished by its herbaceous leaves, 2 to 6 ascendent, not arcuate, racemes per inflorescence, each raceme (3–)5–9 cm long; the rachis of the racemes is usually 1.2–1.5 mm wide, and the spikelets, 1.2–1.4 mm wide, are imbricate along the racemes.

It was not possible to examine the specimen *Foster & D'Achille 12021* of Parque Nacional Manú, which was cited by Tovar (1993) in his treatment of the grasses of Peru.

The specimens *Steinbach 3015*, *Beck 8714*, *17851*, and *Buchtien s.n.* (K, SI, W) differ by having just 4 to 5 racemes per inflorescence and narrow spikelets, sparsely arranged on the racemes.

Representative specimens. BOLIVIA. **La Paz:** Yungas, *Bang 265* (BM, K, MO, W); Prov. Nor Yungas, Coroico 10 km hacia Coripata, *Beck 8714* (K, MO, SI, US); Prov. Nord Yungas, cerca de 10 km al E de Coroico bajando a Caranavi, *Beck et al. 19948* (K, LPB, SI); Nord Yungas, Polo-Polo bei Coroico, *Buchtien 3629* (MO, US, W); Nord Yun-

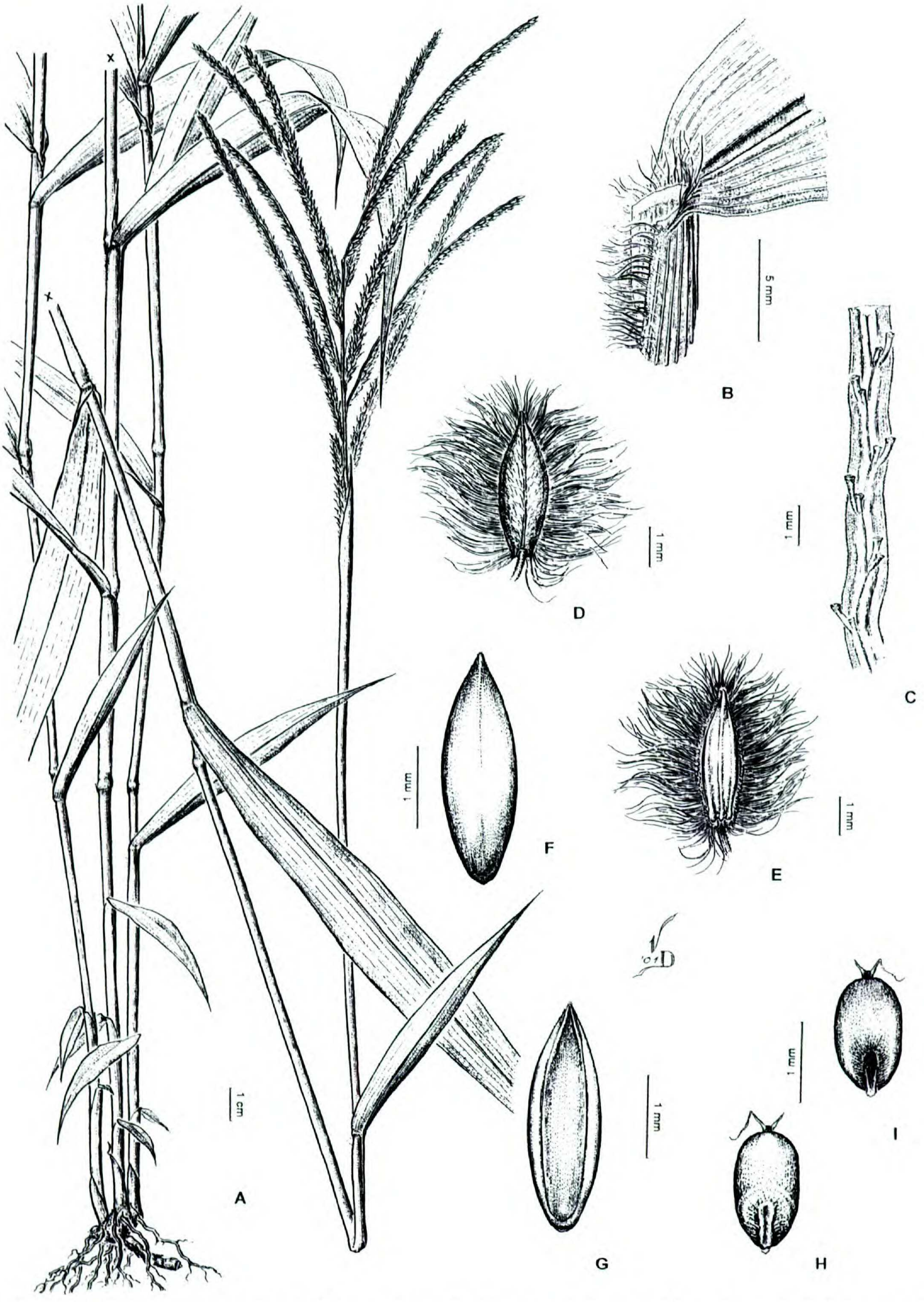

Figure 8. *Paspalum buchtienii*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (A, B based on *Beck et al. 19948*, SI; C–I based on *Hollway & Hollway 712*, US.)

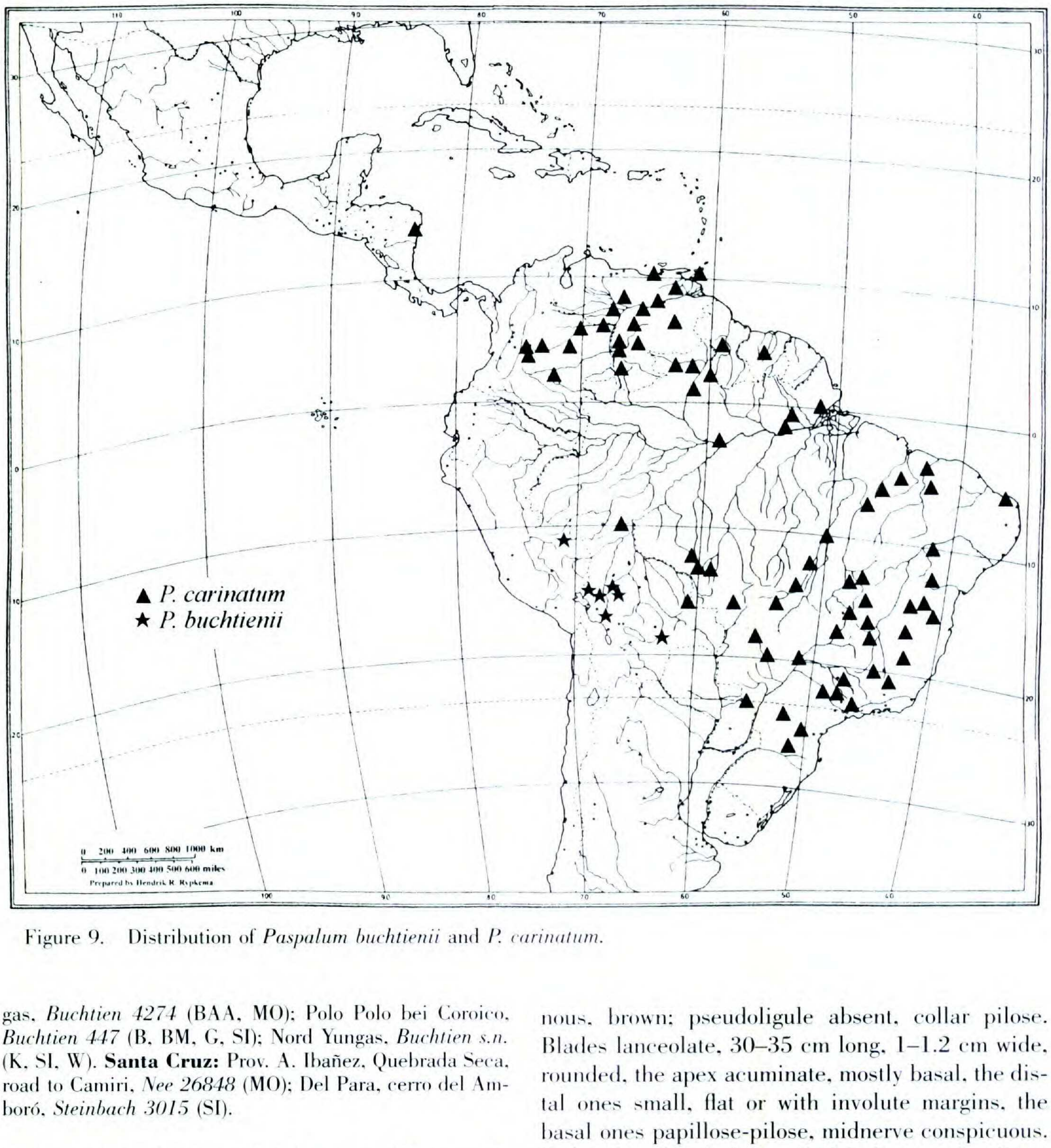
▲ *P. carinatum*
★ *P. buchtienii*
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 9. Distribution of *Paspalum buchtienii* and *P. carinatum*.

gas, *Buchtien 4274* (BAA, MO); Polo Polo bei Coroico, *Buchtien 447* (B, BM, G, SI); Nord Yungas, *Buchtien s.n.* (K, SI, W). **Santa Cruz:** Prov. A. Ibañez, Quebrada Seca, road to Camiri, *Nee 26848* (MO); Del Para, cerro del Amboró, *Steinbach 3015* (SI).

4. Paspalum burmanii Filgueiras, Morrone & Zuloaga, Novon 11: 36, fig. 1. 2001. TYPE: Brazil. Goiás: Mun. Niquelândia, 14°25′S, 48°26′W, margem da estrada entre Niquelândia e Macedo, ca. 10 km N Niquelândia, estrada para Macedo, 20 May 1993, *T. S. Filgueiras 2471* (holotype, IBGE!; isotypes, MO!, SI!, SP!, US!). Figure 10.

Rhizomatous perennials, cataphylls pilose; floriferous culms 1.5 m tall, erect, simple; internodes 12–17 cm long, terete, hollow, lignified, glabrous, smooth; nodes compressed, pilose, brown. Sheaths 15–22 cm long, longer than the internodes, papillose-pilose, with the adaxial surface shiny, the margins shortly pilose. Ligules 2 mm long, membranous, brown; pseudoligule absent, collar pilose. Blades lanceolate, 30–35 cm long, 1–1.2 cm wide, rounded, the apex acuminate, mostly basal, the distal ones small, flat or with involute margins, the basal ones papillose-pilose, midnerve conspicuous. Peduncle subincluded, cylindrical, sparsely pilose. Inflorescences terminal, 20–25 cm long, 5–12 cm wide; main axis 15–20 cm long, glabrous; racemes 9 to 11, ascendent and divergent, alternate, the basal ones 7–9 cm long; pulvini densely pilose with short and long hairs; rachis of the racemes 2.7–3 mm wide, flat, foliaceous, ending in a naked point, occasionally in a spikelet, glabrous, green, the midnerve conspicuous and with anastomosed veins, the margins scabrous; pedicels unequal, terete, scabrous; spikelets paired, imbricate and arranged in 4 series. Spikelets ellipsoid, 3.3–4 mm long, 1–1.2 mm wide, pilose. Upper glume 3-nerved, acuminate, membranous, pilose, more densely so toward the base, the margins corky, hairy, with spreading hairs up to 2 mm long. Lower lemma as long as the

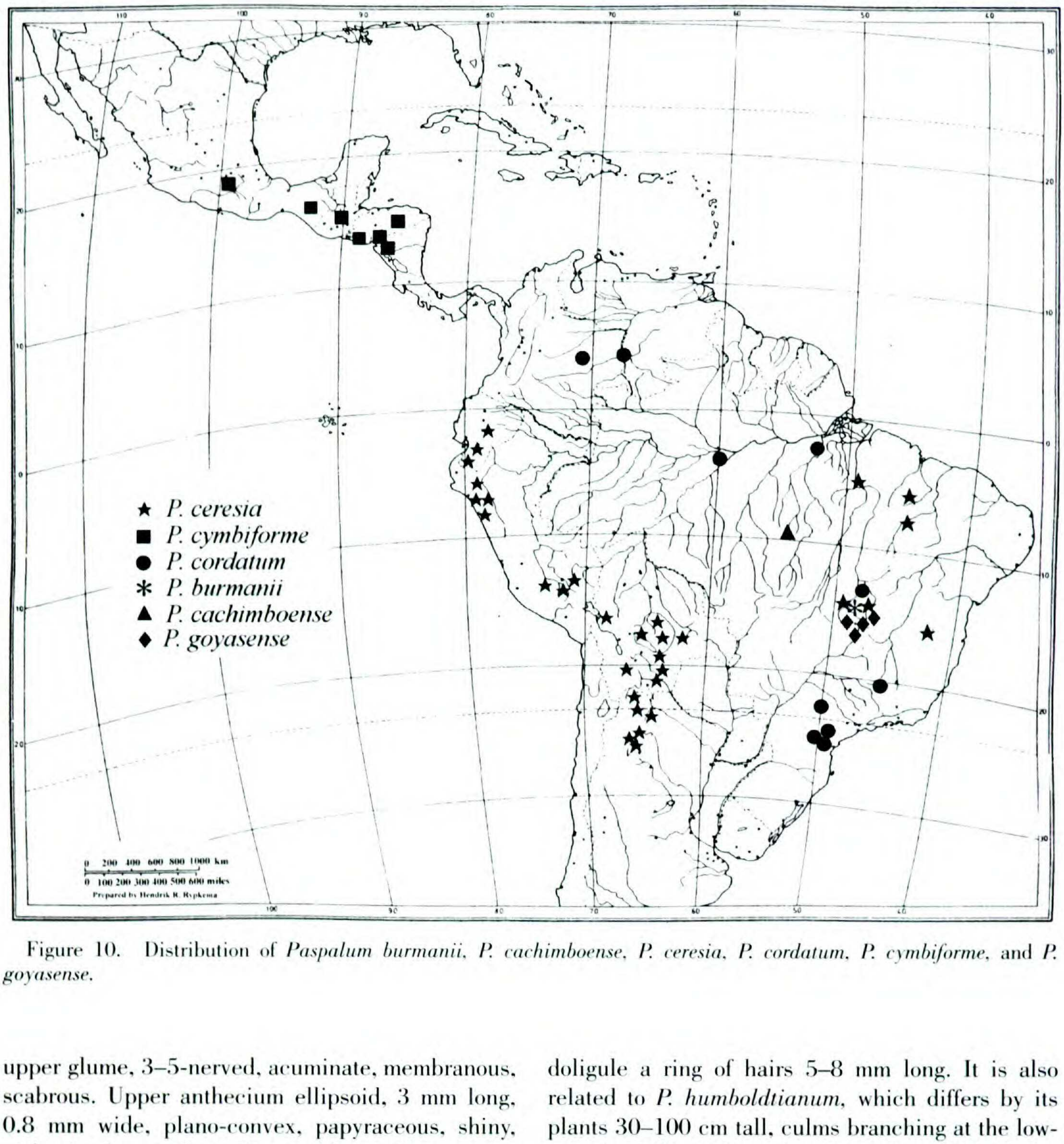
★ P. ceresia
■ P. cymbiforme
● P. cordatum
* P. burmanii
▲ P. cachimboense
◆ P. goyasense
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 10. Distribution of *Paspalum burmanii*, *P. cachimboense*, *P. ceresia*, *P. cordatum*, *P. cymbiforme*, and *P. goyasense*.

upper glume, 3–5-nerved, acuminate, membranous, scabrous. Upper anthecium ellipsoid, 3 mm long, 0.8 mm wide, plano-convex, papyraceous, shiny, with simple papillae all over the surface; upper lemma 5-nerved, with silica bodies and prickles on the upper portion, and bicellular microhairs and macrohairs all over the surface; lodicules 2, 0.2 mm long, conduplicate, hyaline; stamens 3, anthers 2 mm long; stigma plumose. Caryopsis obovoid, 1.5 mm long, 0.7 mm wide, brown; hilum punctiform, basal; embryo less than ½ the length of the caryopsis.

Distribution and habitat. Endemic of Niquelândia, in Goiás, central Brazil, on serpentine soils.

Paspalum burmanii is related to *P. niquelandiae*, which can be separated by its spikelets 2.3–3.3 mm long, with the upper glume almost glabrous or shortly hispid on the surface, racemes 8 to 30, rachis of the racemes up to 1.5 mm wide, and pseudoligule a ring of hairs 5–8 mm long. It is also related to *P. humboldtianum*, which differs by its plants 30–100 cm tall, culms branching at the lower and middle nodes, otherwise unbranched, blades 5–21 cm long, 0.5–1.8 cm wide, evenly distributed along the culms, and inflorescences smaller with 2 to 6 racemes, the rachis of the racemes 1.2–1.5 mm wide.

Representative specimen. BRAZIL. **Goiás:** Niquelândia, a 10 km, *Filgueiras 2477* (SI).

5. Paspalum cachimboense Davidse, Morrone & Zuloaga, Novon 11: 389, fig. 1. 2001. TYPE: Brazil. Mato Grosso: Mun. Colider, estrada Santarém–Cuiabá, BR-163, km 762, Serra do Cachimbo a 30 km de Guarantã, 9°35′S, 54°55′W, 19 Apr. 1983, *M. N. Silva, I. L. Amaral, J. Lima, O. P. Monteiro & J. Coêlho 24* (holotype, MO!). Figure 10.

Caespitose annual; floriferous culms 20–70 cm tall, 1.5 cm diam., red-tinged, geniculate, branching at the middle and upper nodes; internodes hollow, glabrous; nodes brown, glabrous. Sheaths 3–8 cm long, usually shorter than the internodes, densely pilose toward the distal portion, otherwise glabrous, the margins membranous. Ligules membranous, 2–3 mm long; pseudoligule absent; collar papillose-pilose. Blades linear to linear-lanceolate, 14–19 cm long, 0.4–0.6 cm wide, attenuate at the base, the apex acute, densely papillose-pilose on both surfaces and along the margins, midnerve manifest. Peduncles exserted, cylindrical, glabrous. Terminal and axillary inflorescences present, 5–8 cm long, 2–5 cm wide; main axis absent; terminal inflorescences with 1 to 4 approximate racemes, axillary inflorescences usually with a single raceme; pulvini pilose, usually with a membranous bract up to 5 mm long; rachis of the racemes winged, 5–8 cm long, 2–3 mm wide, ending in a naked point, glabrous, the midnerve manifest and the margins membranous, nerveless; pedicels flat, glabrous; spikelets solitary, imbricate and arranged in 2 series. Spikelets long-ellipsoid, 4–4.3 mm long, 1–1.1 mm wide, pale, pilose, occasionally glabrous. Upper glume membranous, rounded at the base, the apex acute, 3-nerved, with one central and two submarginal nerves, pilose at the base, the apex shortly ciliate, the rest of the surface glabrous. Lower lemma glumiform, as long as the upper glume, rounded at the base, 3-nerved, the margins with mixed papillose and not papillose hairs, the apex shortly ciliate. Upper anthecium ellipsoid, 2.2–2.5 mm long, 0.8 mm wide, shorter than the spikelet, stipitate, membranous; upper lemma with simple papillae, macrohairs, and bicellular microhairs toward the distal portion; lodicules 2, conduplicate, hyaline; stamens 3, anthers 1.5 mm long; stigmas 2, plumose. Caryopsis not seen.

Distribution and habitat. Endemic to Serra do Cachimbo in central Brazil, where it is known only from the type collection.

Paspalum cachimboense is a member of section *Pectinata* and closely related to *P. lanciflorum*, which differs by its perennial habit, with simple and erect culms, rachis of the racemes (4–)5–7 mm wide, spikelets (4.8–)5.6–7.2 mm long, and upper anthecium 3.2–4.7 mm long.

6. Paspalum carinatum Humboldt & Bonpland ex Flüggé, Gram. Monogr., Paspalum: 65. 1810 [as "Paspalum carinatus"]. TYPE: Colombia. Without locality, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, B-W not seen; isotypes, BM! photo, SI!, US-2942176!). Figure 9.

Paspalum kappleri Hochst. ex Steud., Syn. Pl. Glumac. 1: 21. 1855 [1853]. *Paspalum carinatum* Humb. & Bonpl. ex Flüggé var. *kappleri* (Hochst. ex Steud.) Döll, in Mart., Fl. Bras. 2(2): 96. 1877. TYPE: Surinam. Without locality, 1843, *F. W. Hostmann 1306* (holotype, P!; isotypes, B!, BM!, G!, K! photo, SI!, MO-102047!, P!, US-2855294!, W!).

Paspalum spissum Swallen, Phytologia 14: 358. 1967. Syn. nov. TYPE: Brazil. Maranhão: Carolina to San Antonio de Balsas, 20–25 Mar. 1934, *J. R. Swallen 4050* (holotype, US-1612651! photo, SI!).

Short-rhizomatous perennial; floriferous culms (25–)40–70 cm long, finely striate, glabrous; nodes brown, glabrous to shortly pilose. Sheaths 5–13 cm long, usually shorter than the internodes, glabrous to hirsute, the margins membranous. Ligules membranous, ca. 0.6 mm long, brown, glabrous; pseudoligule absent or present, when present a ring of white hairs. Blades filiform, 5–20 cm long, 0.5–1(–3) mm wide, involute, erect, mostly basal, rounded at the base, the apex setaceous, papillose-pilose on both surfaces, more densely so toward the base of the adaxial surface, the margins involute, ciliate. Peduncles up to 35 cm long, subterete, glabrous. Terminal inflorescences 6–12 cm long, with a membranous bract often at the basal node; main axis absent or up to 3 cm long, flat, glabrous; pulvini glabrous; racemes 1(or 2), alternate when 2 racemes are present, straight or subfalcate, 5–12 cm long; rachis of the racemes winged, 1.8–2.5(–3.5) mm wide, ending in a naked point, glabrous, the midnerve conspicuous, the margins membranous to hyaline, partially covering the spikelets; pedicels short, flat; spikelets solitary, densely imbricate in 2 series. Spikelets long-ellipsoid, 3.3–5 mm long, 1–1.2 mm wide, dorsiventrally compressed, pale, densely pilose at the basal portion, the apex acute or rounded. Upper glume as long as the spikelet, membranous, 3-nerved, densely pilose on the lower portion, with white hairs up to 3 mm long, shortly pilose on the apex, otherwise scabrous. Lower lemma glumiform, slightly shorter than the upper glume, 3-nerved, pilose on the lower portion, the hairs shorter than those of the upper glume, shortly pilose and scabrous at the apex, the rest of the surface glabrous. Upper anthecium long-ellipsoid, 2.7–3.6 mm long, 1 mm wide, 0.6–1.8 mm shorter than the upper glume, plano-convex, flattened toward the distal portion, membranous, shiny, finely papillose with simple papillae all over the surface; upper lemma with macrohairs, bicellular microhairs, and prickles at the upper portion; upper palea with bicellular microhairs and macrohairs at the apex; lodicules 2, 0.2 mm long, conduplicate, hyaline; stamens 3, anthers 1.6–1.8 mm long; stigmas 2, plumose, of lateral emergence. Caryopsis ovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic, embryo less than half the length of the caryopsis.

Iconography. Smith et al., Fl. Il. Catarinense: 918, fig. e–g. 1982. Renvoize, The Grasses of Bahia: 214, fig. 79, A. 1984. Judziewicz, Fl. Guianas: 469, fig. 83, D. 1990. Rodríguez, Ernstia 8(2–3): 37. 1998.

Common names. "Grama-das-pedras" (Brazil); "Garcita" (Venezuela); "Pa-mac" (Guyana).

Chromosome number. n = 10 (Davidse & Pohl, 1978); n = 40 (Davidse & Pohl, 1972).

Distribution and habitat. Trinidad and Tobago, Nicaragua, Colombia, Venezuela, Guyana, Surinam, Brazil, and Bolivia. It grows in humid savannas on sandy, rocky, or limestone soils, in open places with periodical fires, between 100 and 1600 m.

Paspalum carinatum is related to *P. goyasense* and *P. stellatum*. *Paspalum goyasense* has inflorescences with two distant racemes, rachis of the racemes 1–1.6 mm wide, ending in a developed spikelet, spikelets with the upper glume densely pilose in the lower half, otherwise glabrous, upper glume and lower lemma slightly convex, and blades linear, 8–20 cm long, 0.2–0.4 cm wide. *Paspalum stellatum* has rachis of the racemes wider [(4–)5–10 mm]; when two racemes are present, they are conjugate, upper glume and lower lemma with long ciliate margins, with hairs up to 4 mm long, and the upper anthecium is 0.4–1 mm shorter than the upper glume and lower lemma.

A rudimentary membranous bract is common in the basal portion of the racemes in *Paspalum carinatum*, as was pointed out by Sendulsky and Burman (1978).

Swallen (1967) related *P. spissum* with *P. carinatum*, characterizing the former by its densely papillose-pilose blades 2–3 mm wide, and appressed to the culms. After examination of many specimens and the type collections, we conclude that there is a notorious variation in these characters: filiform blades are mixed with linear blades in several specimens, such as *Valls & Silva 8340*, *Irwin et al. 27667*, and *Swallen 3687*, *4078*; others have filiform blades with papillose-pilose hairs, e.g., *Davidse & Huber 15436* and *Blydenstein & Saravia 1082*. Therefore, *P. spissum* is here considered a synonym of *P. carinatum*.

Although blades are predominantly basal, cauline blades were present in several specimens. This is probably due to the absence of periodical fires, which are associated with its savanna habitat.

Representative specimens. BOLIVIA. **Beni:** Prov. Vaca Diez, Riberalta, *Beck 20564* (K). **Santa Cruz:** Prov. Velasco, San Ignacio, *Bruderreck 2* (K, LPB, SI); Velasco, 5 km E of Comunidad Carmen del Ruiz, *Killeen 2823* (LPB, MO, US). BRAZIL. **Amapá:** Macapá, *Black & Froés 51–12291* (US); Mun. Calcoene, *Mori & Cardoso 17298* (MO). **Bahia:** 15 km S of intersection of Hwy. BR-020 and Rio Roda Velha, *Davidse et al. 12087* (MO); 51 km E of Barreiras along Hwy. BR-242, *Davidse et al. 12124* (MO). **Distrito Federal:** Brazilandia, *Allem & Vieira 1558* (MO); 31 km from Brasília on Anápolis road, *Clayton 4804* (K, US). **Goiás:** Serra Dourada, ca. 15 km S of Goiás Velho, *Anderson 9969* (COL, K, MO); Barra da Lagoa Formosa, *Glaziou 22547* (G, K, P, W); Formosa, *Glaziou 22556* (K, P, US, W). **Maranhão:** Barra do Corda to Grajahú, *Swallen 3643* (P); Barra do Corda to Grajahú, *Swallen 3687* (US); Carolina a San Antonio de Balsas, *Swallen 4078* (US). **Mato Grosso:** Mun. Amambaí, 12 km E Amambaí-Iguatemi, *Allem & Vieira 2007* (MO); ca. 270 km N of Xavantina, *Ramos & Sousa 182a* (K, US). **Minas Gerais:** Metallurgica, Serra de Ouro Branco, *Chase 10306* (US); Serra do Espinhaço, 8 km E de Diamantina, *Irwin et al. 27667* (MO). **Pará:** Belterra, beira do Lago Jurucuí, *Black 47–1777* (US). **Paraná:** Jaguariaiva, *Dusén 10412* (K); Mun. Ponta Grossa, Vila Velha, *Smith et al. 14462* (K, P, SI, US). **Rio Grande do Norte:** Estremoz to Natal, *Swallen 4762* (US). **Roraima:** along Boa Vista–Bonfim road (BR-401), km 40, *Coradin & Cordeiro 696* (MO). **Santa Catarina:** Rio Capinsel, *Dusén 17934* (K, US). **São Paulo:** Casa Branca, *Chase 10595* (MO, US). **Tocantins:** Ilha do Bananal, Mun. Lagoa da Confusão, Reserva indígena Carajá, *da Silva et al. 4082* (IBGE, SI). COLOMBIA. **Arauca:** Estación de Cravo Norte, *Llano 47* (US). **Boyacá:** Llanos Orientales, al sur de El Yopal, *Blydenstein & Saravia 1082* (COL). **Cundinamarca:** savanna of San Martín, 100 mi. SE of Bogotá, *Shaw s.n.* (US-1343796). **Guaviare:** Mun. San José del Guaviare, serranía La Lindosa, *Giraldo-Cañas & López 2566* (MO). **Meta:** Llanos Orientales, entrada de la Serranía San Martín cerca del río Casibare, *Blydenstein & Saravia 847* (COL). **Vichada:** Territorio Faunístico El Tuparro, entre los ríos Tomo y El Tuparro, El Tapón, *Daniel 60* (COL). GUYANA. Weruni-Ituni savanna, *Abraham 83* (K, US); Rupununi District, Lethem, 4 mi. N of Lethem, *Irwin 739* (US). NICARAGUA. **Zelaya:** ca. 5 km S of Bilwaskarma on road to Puerto Cabezas, *Pohl & Davidse 12274* (MO). TRINIDAD AND TOBAGO. Erin savanna, S of Point Fortin, *Soderstrom 1124* (US). VENEZUELA. **Amazonas:** 3–6 km N de Samariapo sobre ruta a Puerto Ayacucho, *Davidse et al. 16775* (MO). **Anzoátegui:** Distr. Bolívar, just S of El Zamuro, Fila El Purgatorio, *Davidse & González 19317* (MO); Distr. Freites, Burro trail betw. San Durrial & Los Pajaritos, *Davidse & González 19802* (MO). **Apure:** S of San Fernando de Apure, *Alba 53-96* (US). **Bolívar:** Dpto. Heres, margen izquierda de la Quebrada Aguas Negra, 10 km al E del tepuy El Zumbador, *Aynard 6019* (MO). **Guárico:** Estación Biológica Los Llanos, del M. A. C. Calabozo, *Aristeguieta 4219* (MO). **Monagas:** 55 km NWN of San Felix & Rio Orinoco along Hwy. 10 to Maturín, *Davidse et al. 4615a* (MO). **Zulia:** Distr. Perijá, 9 km S of the Machiques intersection along the Maracaibo–La Fria Hwy. (Hwy. 6), *Davidse et al. 18355* (K, MO).

7. **Paspalum ceresia** (Kuntze) Chase, Contr. U.S. Natl. Herb. 24: 153. 1925. *Paspalum membranaceum* Lam., Tabl. Encycl. 1: 177. 1791, hom. illeg. *Ceresia elegans* Pers., Syn. Pl. 1: 85. 1805. *Ceresia membranacea* (Lam.) P. Beauv., Ess. Agrostogr.: 9 y 171, t. 5, f. 4. 1812. *Paspalum elegans* (Pers.) Roem. & Schult., Syst. Veg. 2: 290. 1817, comb. illeg. *Panicum ceresia* Kuntze, Revis. Gen. Pl. 3: 360. 1898. TYPE: Peru. Without locality, without collector (holotype, P-LA! photo, SI!; isotypes, P!, US-2855815!). Figures 10, 11.

Paspalum membranaceum Lam. var. *aequiglume* Döll, in Mart., Fl. Bras. 2(2): 94. 1877. TYPE: Bolivia. La Paz: Sorata, 2600–2700 m, Feb.–Apr. 1861, *G. Mandon 1255* (lectotype, designated here, W!; isolectotypes, BM!, G!, K!, P!).

Paspalum membranaceum Lam. var. *inaequiglume* Döll, in Mart., Fl. Bras. 2: 94. 1877. TYPE: Brazil. Goiás: campos between Natividade and Conceição, Feb. 1840, *G. Gardner 4029* (lectotype, designated here, B!; isolectotypes, BM!, G!, K!, P!, US-80085!, W!).

Caespitose, short rhizomatous perennial; rhizomes arcuate, covered by pilose cataphylls; floriferous culms 40–80 cm tall, 0.1–0.2 cm diam., branched or unbranched; internodes 4–12 cm long, terete, hollow, glabrous; nodes glabrous. Sheaths 3–12 cm long, glaucous, glabrous to sparsely pilose on the distal portion, the margins membranous, glabrous. Ligules 1–2 mm long, membranous, truncate, glabrous; pseudoligule absent, collar glabrous. Blades filiform, linear-lanceolate or lanceolate, 7–21 cm long, 0.3–1.5(–2) cm wide, flat or with involute margins, rigid, slightly divergent, glaucous, glabrous to sparsely papillose-pilose toward the base of the adaxial surface, the margins glabrous to sparsely papillose-pilose. Peduncles subincluded to exserted, up to 35 cm long, cylindrical, glabrous. Terminal inflorescences exserted, 4–12 cm long, 2–10 cm wide; main axis absent or up to 7 cm long, triquetrous, glabrous; pulvini glabrous or shortly pilose, without papyraceous bracts; racemes (1)2 to 7, ascendent, divergent and alternate, distant; rachis of the racemes 2–7 cm long, 6–10 mm wide, ending in a naked point, glabrous, green or purple at the middle portion, hyaline at the margins, these brown or ferruginous; pedicels up to 0.4 mm long, flat, hispidulous; spikelets solitary and imbricate in 2 series. Spikelets long-ellipsoid, (3–)3.4–3.6 mm long, 1.2–1.4 mm wide, acute, villous, early deciduous; upper glume and lower lemma subequal. Upper glume hyaline to membranous, 3-nerved with one central and two marginal nerves, densely pilose at the base and along the margins, the hairs silky, ascendent, up to 4 mm long. Lower lemma glumiform, hyaline, pilose, with 2 submarginal nerves. Upper anthecium long-ovoid, 2.6–3.6 mm long, 1–1.2 mm wide, not stipitate, hyaline and shiny, white, scabrous and pilose toward the apex; upper lemma with prickles, macrohairs, bicellular microhairs, and silica bodies at the apical portion, upper palea with bicellular microhairs and macrohairs at the apex; lodicules absent; stamens 3, anthers 2.4–2.8 mm long. Caryopsis obovoid, 1.2–1.6 mm long, 0.8 mm wide; hilum punctiform, embryo ½ the length of the caryopsis.

Distribution and habitat. Ecuador, Peru, Brazil, Paraguay, Bolivia, and Argentina, in rocky mountain slopes and open fields on sandy and rocky soils, between 300 and 3000 m.

Paspalum ceresia is related to *P. stellatum*, a species with filiform leaves 8–27 cm long, 0.1–0.3 cm wide, 1 (occasionally 2) racemes, 1 or 2 papyraceous bracts in the basal pulvini, radiate hairs on the pedicels, lodicules present, and upper anthecium stipitate. *Paspalum ceresia* is also similar to *P. trachycoleon*, a species from Central America, Venezuela, Colombia, and southern Brazil, which is characterized by the rachis of the racemes 4–6 mm wide, spikelets paired, with an annular thickening at the base, and lower lemma membranous, 3-nerved.

A single collection was examined from Paraguay, *Isabell s.n.* at P, a specimen without any information about collection date or locality; it is possible this specimen was mislabeled, considering the distribution range of the species.

There is considerable variation in the leaf shape, from filiform to linear and rigid, up to 0.3 cm wide, in the specimens *Oliveira et al. 305, 598, Pinheiro & Carvalho 142, 517, 625, Gardner 4029, Brooks et al. 125, Eiten & Eiten 4418, 3777, 10789,* and *Swallen 3772,* filiform and lanceolate in a single specimen, e.g., *Souza et al. 5548, Filgueiras 2280,* or with lanceolate leaves, up to 2 cm wide, as in *Nee 40372.*

Doell (1877) described variety *aequiglume* and variety *inaequiglume* of *P. membranaceum* on the basis of variation of the upper glume and lower lemma length, a variable character according the degree of maturity of the spikelets. This author cited the specimens *Rhodé s.n.* and *Mandon 1255* as syntypes of variety *aequiglume*, of which *Mandon 1255* agrees with the protologue and is here selected as lectotype of this taxon. Also, Doell (1877) cited *Pohl s.n.* and *Gardner 4029* as syntypes of variety *inaequiglume*, of which *Gardner 4029* is here chosen as lectotype of the variety.

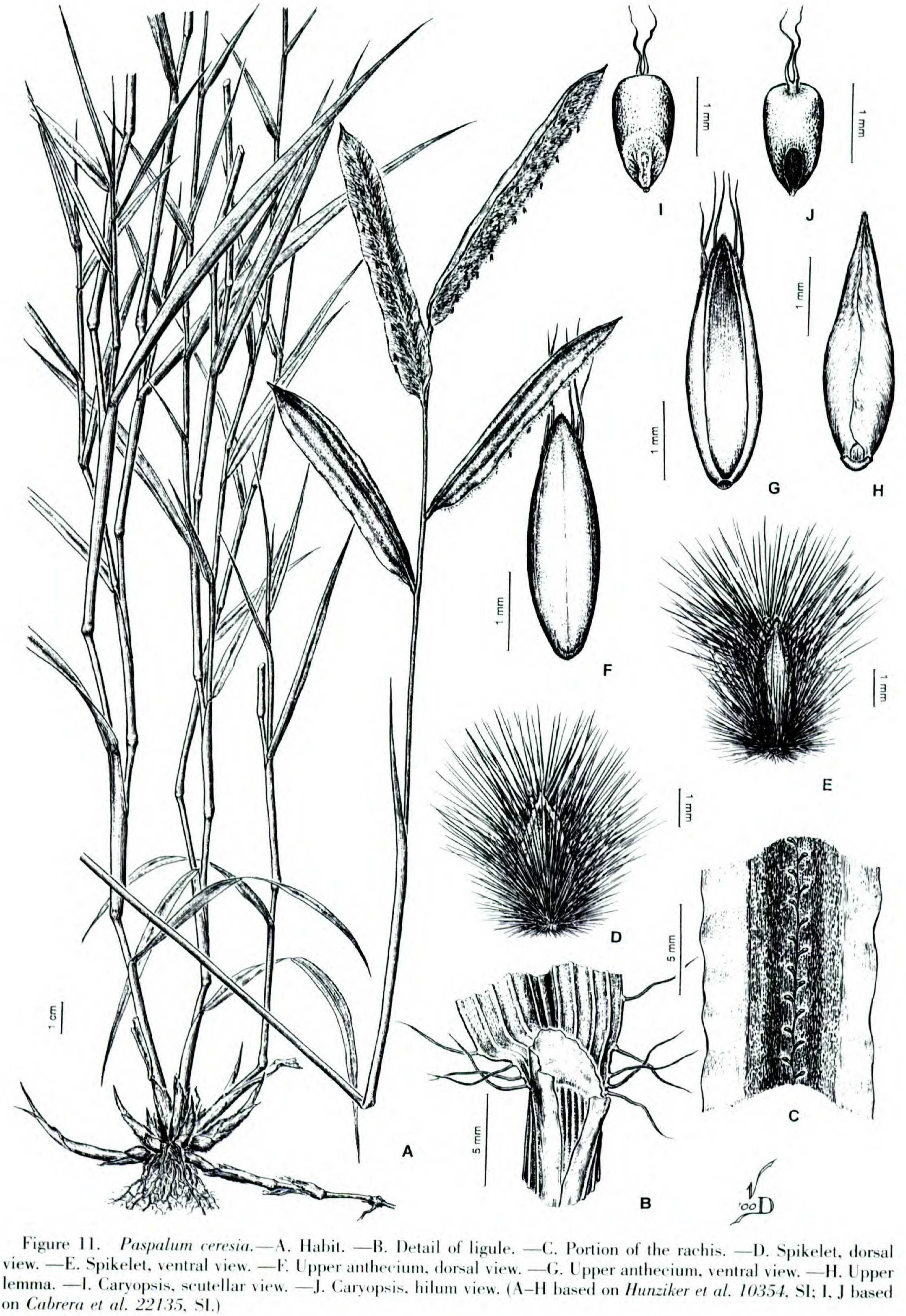

Figure 11. *Paspalum ceresia.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper lemma. —I. Caryopsis, scutellar view. —J. Caryopsis, hilum view. (A–H based on *Hunziker et al. 10354*, SI; I, J based on *Cabrera et al. 22135*, SI.)

Representative specimens. ARGENTINA. **Jujuy:** Dpto. Santa Bárbara, El Fuerte, *Cabrera & Fabris 22730* (US); Dpto. Humahuaca, Sierra de Zenta, *Venturi 8320* (K, LIL, MO, P, SI, W). **Salta:** Dpto. Candelaria, Unquillo, *Schreiter 9256* (LIL); Dpto. Guachipas, Alemanía, *Venturi 9905* (MO, W). **Tucumán:** San Pedro de Colalao, *Dinelli 12876* (LIL). BOLIVIA. **Chuquisaca:** 15 km S of Padilla, *Renvoize & Cope 3870* (K, MO). **Cochabamba:** Prov. Quillacollo, ca. 45 km hacia Oruro, *Beck 4025* (US). **Potosí:** Prov. Charcas, Qda. Llama Chaqui, *Mostacedo 314* (MO). **Santa Cruz:** Prov. Caballero, 15 km arriba de San Juan de Portero, *Killeen & Vargas 4152* (MO); Prov. Florida of Río Mairana, 3 km N of hwy. at Yerba Buena, *Nee 40372* (K, MO). **Tarija:** Tarija, *Fiebrig 2664* (SI). BRAZIL. **Goiás:** Faz. Buracão, ca. 35 km (by road) N of Goianésia, *Brooks et al. 125* (K, MO, NY); Niquelândia, ca. 18 km W de Niquelândia, *Filgueiras 2280* (MO, US); Niquelândia, 2 km da estrada de Chao para o Macedo Velho, *Oliveira et al. 305* (SI); Mun. Niquelândia, Macedo, ca. 0.1 km abaixo da mina de niquel, *Oliveira et al. 598* (US). **Maranhão:** Mun. Lorêto, Ilha de Balsas region, *Eiten & Eiten 3777* (K, US), *4418* (K); Barra do Corda to Grajahú, *Swallen 3772* (K, P). **Minas Gerais:** Retiro ca. 16 km da cidade em direção a Mato Verde, *Souza et al. 5548* (K). **Pará:** Estreito-Marabá, km 1, 4 Abr. 1974, *Pinheiro & Carvalho 142* (US); km 2, *Pinheiro & Carvalho 517, 625* (US). ECUADOR. **Azuay:** valley of the Río Paute, between Paute and Cuenca, between Ríos Azogues & Gualaceo, *Camp 2332* (K, P, US, W). **Loja:** road San Pedro de la Bendita (W of Catamayo)–El Cisne, *Øllgaard et al. 90721* (MO); 6 km W of Colaisaca on road to Sozoranga, *Peterson & Judziewicz 9478* (K, MO, US). PARAGUAY. **Without department:** without locality, *Isabell s.n.* (P). PERU. **Apurimac:** Prov. Abancay, Cunyac, *Chávez 3217* (MO). **Cajamarca:** Prov. Chota, El Tingo, a 6 km sobre la carretera Cochabamba–Huambos, *Sánchez Vega 2332* (SI, US); Dpto. Cajamarca, 4 km E of Celendin on road to Balsas, *Hutchinson & Wright 5194* (G, K, MO). **Cuzco:** Prov. Anta, Mollepata, *Vargas 19047* (MA). **Huancavelica:** entre Izcuchaca y Acoria, *Tovar 1020* (US).

8. **Paspalum cordatum** Hackel, Ark. Bot. 9(15): 5. 1910. TYPE: Brazil. Paraná: Rio Tibagy in der Nähe des Städtchens Ponta Grossa, am Rande eines Sumpfes, 7 Ene. 1904, *P. K. H. Dusén 3248* (holotype, W!; isotypes, G!, US-2942131!). Figures 10, 12.

Robust, rhizomatous perennials with long, arcuate rhizomes; floriferous culms erect, 100–130 cm tall, 0.4–1 cm diam., unbranched; internodes finely striate, hollow, glabrous; nodes compressed, glabrous, brown. Sheaths usually longer than the internodes, the lower ones overlapping, loose, densely hirsute on the basal portion or glabrous, the inner surface shiny, brown to red-tinged, the margins membranous. Ligules membranous, 1–1.3 mm long, brown, glabrous; pseudoligule a ring of dense, rigid hairs up to 6 mm long; collar densely pilose. Blades linear, 10–50 cm long, 0.5–1.1 cm wide, flat, the margins involute, ascendent and rigid, densely villous on both surfaces, attenuated at the base, the apex beaked. Peduncles exserted, up to 45 cm long, subterete, glabrous. Terminal inflorescences exserted, 7–18 cm long, 6–18 cm wide, subdigitate; main axis up to 4 cm long, wavy, glabrous to sparsely pilose; pulvini pilose; racemes 5 to 10, 12–16 cm long, ascendent, alternate to subopposite, ending in a naked point; rachis of the racemes flat, 1.8–2.4 (–3.2) mm wide, glabrous and green, the margins shortly winged, scaberulous; pedicels short, glabrous; spikelets solitary, densely imbricate in 2 series. Spikelets ovoid, 4–5(–6) mm long, 2.5–3.5 mm wide, dorsiventrally compressed, pale, winged, cordate, the apex acute. Upper glume as long as the spikelet, membranous, glabrous, cordate, 5-nerved, with 3 central nerves reaching the apex, and 2 lateral nerves only notorious at the base. Lower lemma 3.4–3.6(–5) mm long, 1 mm wide, subcordate, 3-nerved, the margins with rigid and thick papillose-pilose hairs, not winged, shortly pilose. Upper anthecium ellipsoid, membranous, 3–3.2 mm long, 0.8 mm wide, shorter than the spikelet, plano-convex, pilose on the upper margins, pale; upper lemma with simple papillae all over the surface, and bicellular microhairs, macrohairs, and silica bodies toward the apex; upper palea with simple papillae, bicellular microhairs, and macrohairs on the upper portion; lodicules 2, ca. 0.4 mm long, conduplicate, hyaline, glabrous; stamens 3, anthers 1.6 mm long; styles 2, stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. This species grows in southern Brazil, in the states of Amazonas, Paraná, Goiás, Minas Gerais, and São Paulo, also in Colombia, in the states of Meta and Vichada, in open areas, lowlands, and swamps.

Rodríguez (1998) considered *Paspalum cordatum* as a synonym of *P. pectinatum* without indicating the criteria for such a decision. Both species share spikelets with the upper lemma not winged and with conspicuous rigid, papillose-pilose hairs on the margins. Nevertheless, we consider *P. pectinatum* a different entity by including specimens with 2, occasionally 3, conjugate racemes, 2–8 cm long, per inflorescence. Additionally, plants, which grow in savannas or open fields on sandy or rocky soils, are smaller and more densely caespitose than those of *P. cordatum*, with lower sheaths burnt by fire.

Paspalum cordatum is also related to *P. imbricatum*, this species with glabrous spikelets and lower lemma winged.

Note that in the specimens *Blydenstein 939* and *Cabrera 2278*, the rachis of the racemes is 3–3.2 mm wide, with crenate margins, and spikelets are bigger, 5.2–6 mm long.

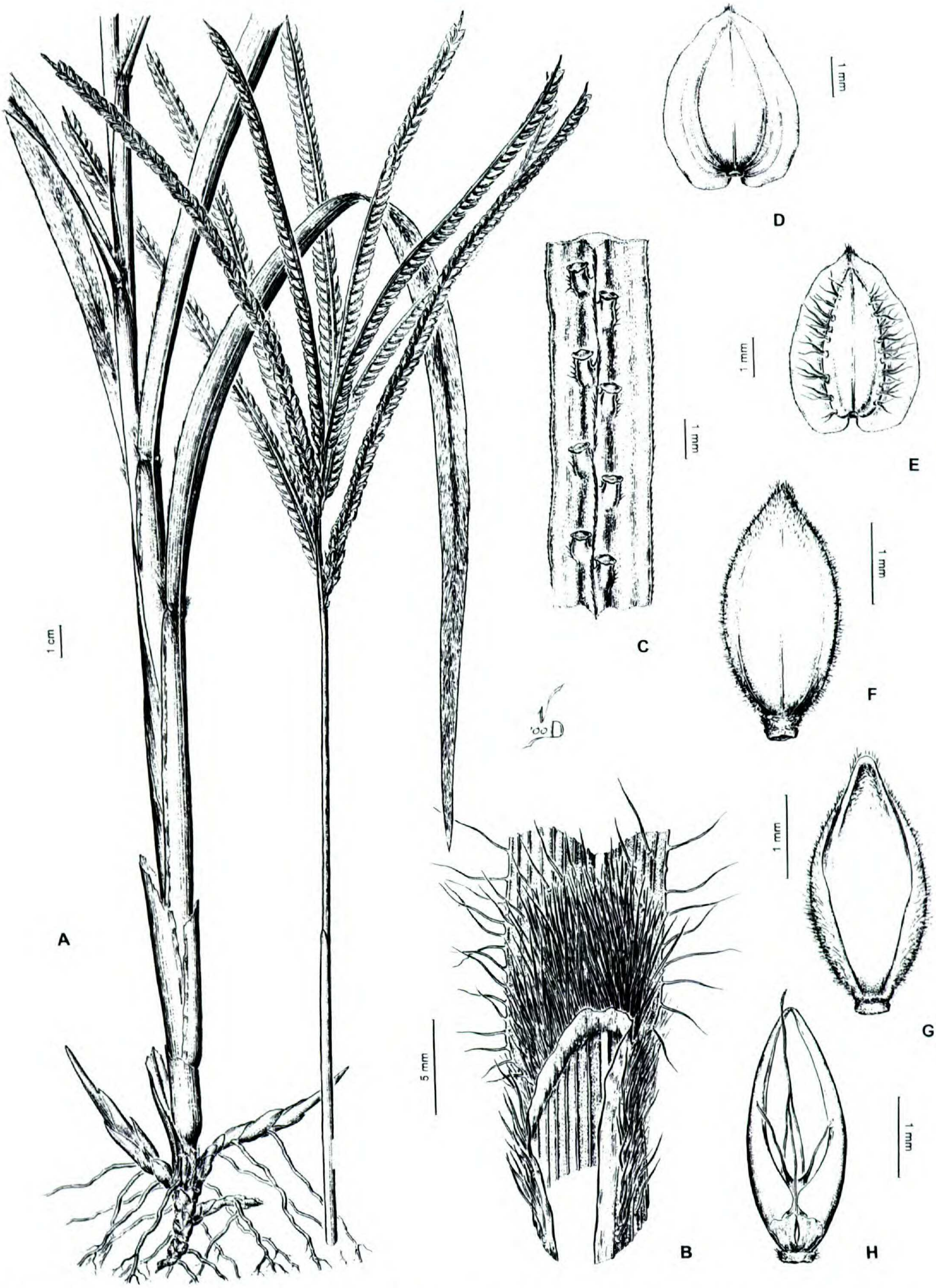

Figure 12. *Paspalum cordatum*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper lemma, lodicules, and gynoecium. (Based on *Hatschbach & Renvoize 5276*, US.)

Representative specimens. BRAZIL. **Amazonas:** Transamazon Hwy., 53 km W de Aripuana River, *Calderón et al. 2708* (MO, US-3082134). **Goiás:** Jataí, *Macedo 1543* (US). **Minas Gerais:** without locality, *Weddell 1699* (G, P). **Paraná:** Turma, in paludosis, *Dusén 9109* (BM, US); Jaguariaiva, *Dusén 16174* (BM, G, SI, US); Mun. Campo Largo, Serra S. Luis, *Hatschbach et al. 12097* (K, MBM); Mun. Pirai do Sul, Serra das Furnas, *Smith et al. 14579* (K, P, SI, US); Mun. Senges, Faz. Morungava, Rio Funil, *Smith et al. 14858* (K, P, US); Ponta Grossa, Faz. Cambujan, *Brade 19638* (US). **São Paulo:** Estação Florestal de Paraguaçu Paulista, 6 km N of city, *Clayton 4631* (K, US). COLOMBIA. **Meta:** Llanos orientales, Hato Pozones, *Blydenstein 939* (COL, MO). **Vichada:** Caño Urimica, *Cabrera 2278* (COL).

9. **Paspalum cymbiforme** E. Fournier, Mexic. Pl. 2: 5. 1886. TYPE: Mexico. México: San Pablo, *F. M. Liebmann 226* (lectotype, designated by Chase (1929: 20), C not seen). Figure 10.

Shortly rhizomatous perennial; floriferous culms 60–90 cm tall, branching at the middle nodes or simple; internodes terete, striate, glabrous; nodes brown, covered by ascendent white hairs. Sheaths longer than the internodes, striate, glabrous, the margins ciliate at the lower portion. Ligules brown, membranous, 1–1.2 mm long; pseudoligule a ring of hairs. Blades linear, 5–19(–24) cm long, 0.2–0.5(–0.8) cm wide, flat, glabrous or shortly pilose on the adaxial surface, the margins with tuberculate hairs up to 5 mm long, shortly pseudopetiolate, pseudopetiole with short, white hairs. Peduncles exserted, 15–20 cm long, terete, pilose. Terminal inflorescences 8–12 cm long, 3–4 cm wide; main axis absent or up to 5 cm long, shortly hispid or glabrous; pulvini pilose; racemes 1 to 4, 3–8 cm long, alternate, ending in a naked point; rachis of the racemes 2–2.8 mm wide, green and tinged with purple, the midnerve manifest, wings short, hyaline, nerveless; pedicels ca. 0.3 mm long, pubescent, spikelets paired and imbricate in 2–4 series, usually the lower spikelet aborted. Spikelets long-ellipsoid, 3 mm long, 1 mm wide, acute, pilose, pale. Upper glume hyaline to membranous, 3-nerved, with one central and two submarginal conspicuous nerves, the margins corky, with long, ± ascendent hairs, up to 3 mm long, and with small hairs on the basal portion. Lower lemma as long as the upper glume, membranous, 3-nerved, shortly pilose toward the apex, otherwise glabrous, depressed on the basal portion. Upper anthecium long-ellipsoid, 2.2 mm long, 0.8 mm wide, pale, membranous; upper lemma 3-nerved, finely papillose and with prickles, silica bodies, and bicellular microhairs at the apex; upper palea papillose, with macrohairs and bicellular microhairs at the apex; lodicules 2, 0.2–0.3 mm long, conduplicate, hyaline; stamens 3, anthers 1.5 mm long; stigma plumose, lateral. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 21, fig. 4. 1929.

Distribution and habitat. Found from southern Mexico to Nicaragua, on mountain slopes on rocky soils, between 750 and 1300 m.

This species differs from *P. humboldtianum* and *P. polyphyllum* by the rachis 2–2.8 mm wide (vs. 1.2–1.5 mm in *P. humboldtianum* and 1–1.2 mm in *P. polyphyllum*), and by the presence of hairs at the apical portion of the lower lemma.

The specimen *Davidse et al. 31637* has 2 to 7 racemes per inflorescence.

Representative specimens. EL SALVADOR. **La Libertad:** *Eggler 639* (US). **Santa Ana:** Mun. Candelaria de la Frontera, Cerro El Yupe, *Linares 3663* (MEXU). GUATEMALA. **Zacapa:** lower slopes of Sierra de las Minas, along trail above Río Hondo, *Steyermark 29550* (US). HONDURAS. **Distrito Federal:** Llamapa, SW of Talanga, Rancho Santa Regina de Archaga, *Pohl & Gabel 13531* (MO). **Francisco Morazán:** 26 km N of Pespire along Hwy. 1 to Tegucigalpa, *Davidse & Pilz 31637* (MO); region of Las Mesas, *Swallen 10809* (MO, US), *10747* (US). **Olancho:** El Espino, 8 km NE de Catacamas, *Enamorado 23* (MO). MEXICO. Consoquitla, *Liebmann 225* (MO); Mun. Frontera Comalapa, 6–8 km E of Frontera Comalapa along road to Ciudad Cuauhtemoc, *Breedlove 39106* (MEXU). **Chiapas:** Mun. Ixtapa, along Mexican Hwy. 190 in the Zinacantán Paraje of Muctajoc, *Breedlove 13822* (MEXU, US). **Mexico:** Temascaltepec, Bejucos, *Hinton 2532* (BAA, K). NICARAGUA. **Chinandega:** Volcán Casita, Montaña del Cielo, 12°42′N, 86°58′W, *Rueda & Aller 1200* (MO).

10. **Paspalum eucomum** Nees ex Trinius, Sp. Gram. 1: pl. 110. 1828. *Paspalum eucomum* Nees, Fl. Bras. Enum. Pl. 2: 37. 1829, hom. illeg. TYPE: Brazil. Without locality, *F. Sellow s.n.* (holotype, LE not seen; isotypes, BM!, K! photo, SI!, P!, US-2854694!, US-2854695!). Figures 13, 14.

Paspalum eucomum Nees ex Trin. var. *pilosior* Döll. in Mart., Fl. Bras. 2(2): 65. 1877. TYPE: Brazil. Minas Gerais: Lagoa Santa, *E. Warming s.n.* (holotype, not located; isotype, US-2854696!).

Paspalum splendens Hack., Oesterr. Bot. Z. 51: 238. 1901. TYPE: Brazil. Goiás: without locality, *A. F. M. Glaziou 22554* (lectotype, designated here, W!).

Caespitose, shortly rhizomatous perennial; floriferous culms 60–110 cm tall, 0.2–0.3 cm diam., erect, ascendent, unbranched, occasionally branching at the middle nodes; internodes 6–15 cm long, striate, glabrous; nodes glabrous. Sheaths usually longer than the internodes, 8–25 cm long, overlapping, glabrous or papillose-pilose all over the sur-

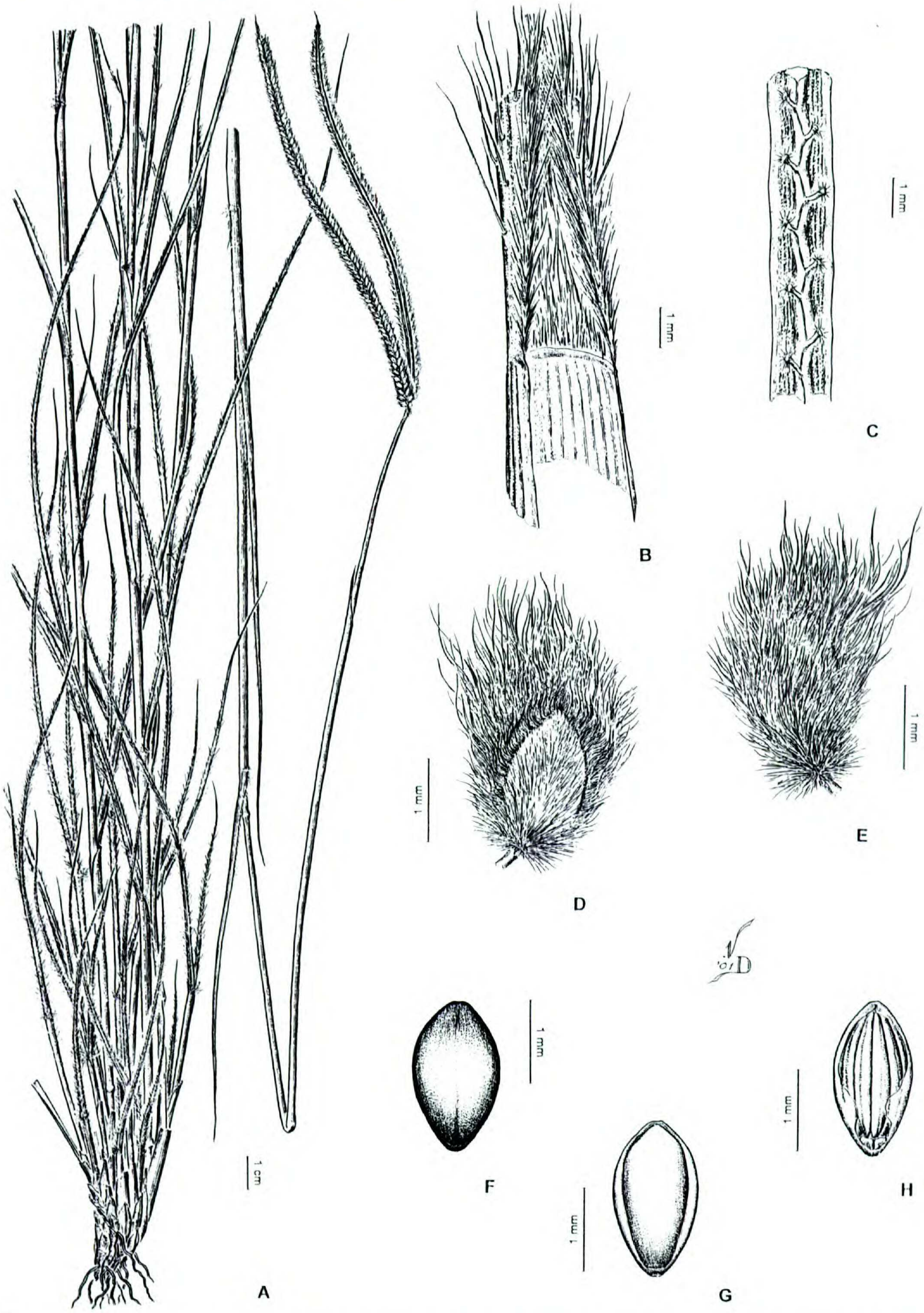

Figure 13. *Paspalum eucomum.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and anthers. (Based on *Chase 9097,* US.)

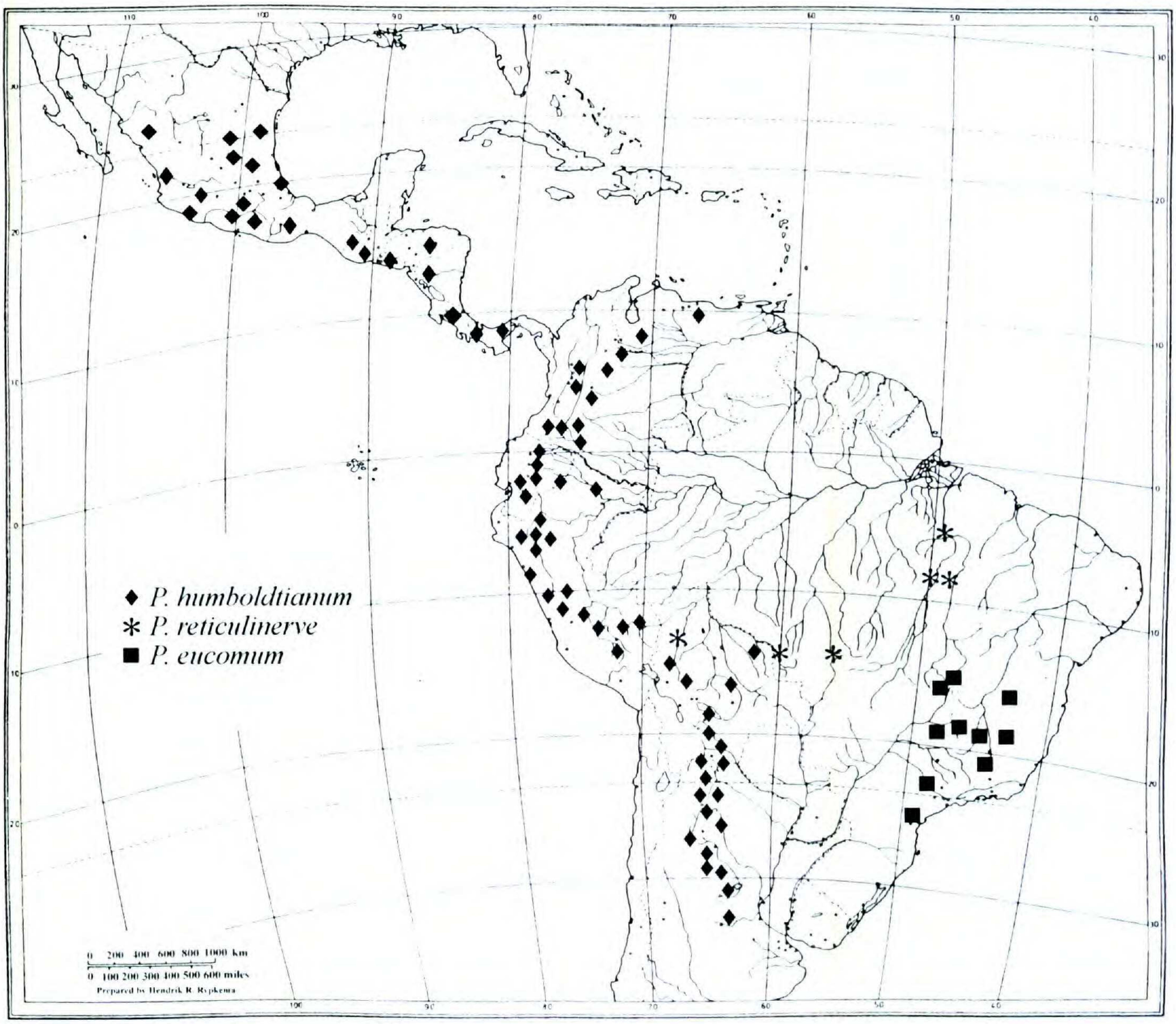
◆ *P. humboldtianum*
* *P. reticulinerve*
■ *P. eucomum*
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 14. Distribution of *Paspalum eucomum*, *P. humboldtianum*, and *P. reticulinerve*.

face or only at the distal portion, the hairs up to 5 mm long, the margins membranous, glabrous or with one margin ciliate. Ligules membranous, 0.2–0.5 mm long, truncate, brown, glabrous; pseudoligule a ring of white hairs up to 2.5 mm long. Blades filiform, 10–30 cm long, 0.2–0.5 cm wide, erect or flexuous, rigid and involute, narrow, the apex setaceous, adaxial surface with conspicuous papillae and tuberculate hairs, abaxial surface glabrous or both surfaces densely hirsute. Peduncles exserted, up to 30 cm long, subterete, pale or purple, glabrous. Terminal inflorescences conjugate; main axis absent; pulvini pilose, with a bract usually present; racemes 2, (4–)6–17 cm long, occasionally with a third approximate raceme, ascendent, divergent, ending in a naked point; rachis of the racemes 1.5–2.5(–4) mm wide, shortly winged, glabrous, green to purple, the margins hyaline, nerveless; pedicels short, flat, and sparsely pilose; spikelets solitary, densely imbricate in 2 series. Spikelets ellipsoid, 2.5–3 mm long, 1.4–1.6 mm wide, dorsiventrally compressed, acute, densely pilose toward the base and the margins, pale or tinged with purple. Upper glume as long as the spikelet, membranous, 3-nerved, the base and margins covered with white, rigid hairs, the rest of the surface with short and appressed hairs. Lower lemma glumiform, slightly shorter than the upper glume, 3-nerved. Upper anthecium obovoid, 2.4–3 mm long, 1.2 mm wide, membranous, pale, shiny, rounded at the apex, smooth; lodicules 2, ca. 0.3 mm long, membranous, conduplicate; stamens 3, anthers 1.5 mm long; stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. Restricted to central and southern Brazil in the states of Goiás, Minas Gerais, São Paulo, Paraná, and in the Federal District. It grows in cerrados, in open fields on sandy soils, between 700 and 1100 m.

Paspalum eucomum is closely related to *P. mal-*

meanum. The latter species mainly differs by the spikelets 1.6–2 mm (vs. 2.5–3 mm long); also, *P. malmeanum* grows in Bolivia and Mato Grosso, on flooded soils, while *P. eucomum* occurs in central and southern Brazil, usually in drier settings. It should be pointed out that spikelet size, 2.3–2.5 mm long, is intermediate between both species in *Macedo 351*, *Sendulsky 1239*, and *Glaziou 17406*. These species are here considered as different entities until more material becomes available.

Chase (ined.) distinguished *P. eucomum* from *P. splendens* by the spikelet size (2.5 mm long vs. 3 mm), rachis width (1.5–2 mm vs. 2–3.5 mm), and general aspect of plants (delicate vs. robust). Upon study of many specimens, we conclude that there is a gradation in these characters, which are not useful to distinguish both species.

Chase (ined.) and Sendulsky and Burman (1980) pointed out that *Glaziou 22555* is one of the syntypes of *Paspalum splendens*. Nevertheless, Hackel (1901) cited, as syntypes, the specimens *Glaziou 22552*, *22553*, and *22554*, of which *Glaziou 22554* agrees with the original diagnosis and is here designated as lectotype of the species.

The rachis of the racemes is exceptionally wide, up to 4 mm, in the specimens *Dias et al. 67* and *Weddell 2556*.

Chase (ined.) studied, at B, two specimens collected by *Sellow, 1238* and *1336*, which were examined by Nees and probably represent isotypes of *P. eucomum*. Duplicates of these collections from US were identified by us as *P. eucomum*.

Representative specimens. BRAZIL. **Distrito Federal:** Brasília, *de Jesus 3* (US); Brasília, *Dias et al. 67* (MO); E margin of Lagoa Paranoá, *Irwin et al. 15328* (K, MO, US). **Goiás:** without locality, *Glaziou 22551* (B, G, K, P), *Glaziou 22555* (K, MO, P, US). **Minas Gerais:** between Sucupira and Omega, S of Uberlandia (Uberabinha), *Chase 11200* (BM, K, US, W); Serra de S. José, *Glaziou 17406* (P, US, W); without locality, *Macedo 351* (US); Conceição do Mato Dentro, Rodovia Belho Horizonte, 10 km antes de Chapéu do Sol, *Sendulsky 1239* (US). **Paraná:** Porto Amazonas, *Dusén 18065* (BM, MA, MO, P, SI). **São Paulo:** Mun. Botucatú, 18 km N of Botucatú, 14 km E of São Manuel, *Gottsberger 1043* (US). **Without state:** without locality, 1844, *Weddell 2556* (P).

11. Paspalum goyasense Davidse, Morrone & Zuloaga, Novon 11: 391, fig. 2. 2001. TYPE: Brazil. Goiás: 25 km E de Cabeceiras (ca. 4 km E of Goiás–Minas Gerais), cerrado, 1000 m, 19 Nov. 1965, *H. S. Irwin, R. Souza & R. Reis dos Santos 10524* (holotype, MO!; isotype, US-2529124!). Figure 10.

Caespitose perennial; culms 40–65 cm tall, erect, unbranched, few-noded; internodes 2–3, 6–20 cm long, 0.1 cm diam., terete, hollow, glabrous; nodes brown, densely pilose. Sheaths 3–10 cm long, mostly basal, papillose-pilose or hispid, the margins membranous. Ligules 0.5–0.9 mm long, membranous, brown, glabrous; pseudoligule absent; collar pilose. Blades linear, 8–20 cm long, 0.2–0.4 cm wide, mostly basal, flat or with involute margins, ascendent and rigid, rounded at the base, the apex acute, densely papillose-pilose on both surfaces, the margins ciliate. Peduncles long exserted, up to 30 cm long, filiform, pale or tinged with purple. Inflorescences terminal, exserted, with 2 racemes, occasionally with a single raceme or with a third raceme present; main axis up to 3 cm long, flat, smooth, glabrous, occasionally absent; pulvini glabrous, with a squamiform bract; racemes alternate, ascendent and divergent, ending in a developed spikelet; rachis of the racemes flat, straight, (2–)3–7 cm long, 1–1.6 mm wide, glabrous, the midnerve pale to green, the wings hyaline, nerveless, pale to purple; pedicels short, glabrous; spikelets solitary, imbricate and arranged in 2 series. Spikelets long-ellipsoid, 4–5 mm long, 1–1.1 mm wide without the hairs, plano-convex to slightly biconvex, acute, smooth, pilose; upper glume and lower lemma densely pilose on the lower half with white hairs, otherwise glabrous, the margins with papillose hairs, up to 2.5 mm long, reduced toward the apex. Upper glume as long as the spikelet, acute at the apex, with or without a short tuft of hairs, membranous, 3-nerved, with one central and two submarginal nerves. Lower lemma glumiform, as long as the spikelet or slightly shorter, 3–5-nerved. Upper anthecium long-ellipsoid, 3.2–4 mm long, 0.9 mm wide, 0.7–1 mm shorter than the spikelet, plano-convex, membranous to chartaceous; upper lemma with small papillae regularly distributed, and a tuft of macrohairs at the apex; lodicules 2, ca. 0.3 mm long, conduplicate; stamens 3, anthers 2 mm long; stigma plumose. Caryopsis long obovoid, 2 mm long, 0.9 mm wide; hilum elliptic; embryo ⅓ as long as the caryopsis.

Distribution and habitat. Endemic to central Brazil, where it grows in the Federal District and in the state of Goiás, in cerrados between 900 and 1200 m.

Paspalum goyasense is a close species of *P. carinatum*, the latter with filiform leaves, inflorescences usually with a single raceme, rachis of the racemes 1.8–2.5(–3.5) mm wide, spikelets with long hairs rising from the lower third, conspicuously scabrous on the rest of the surface, and apex of the upper glume and lower lemma dorsiventrally compressed and flat.

Representative specimens. BRAZIL. **Distrito Federal:** Brasília, *Irwin et al. 10257* (MO, US); 10 km W of Taguatinga, ruta a Braslandia, *Irwin et al. 10654* (MO, UB, US); Chapada da Contagem, ca. 20 km N de Brasília, *Irwin et al. 9648* (MO, US); Brasília, *Irwin et al. 9658* (MO, US); Brasília, Lago Sul, *Zuloaga 3835* (SI). **Goiás:** without locality, *Glaziou 22441* (G, US, W), *Glaziou 22443* (G, US, W); Serra dos Pirineus, 14 km S de Corumbá de Goiás, 16°S, 49°W, *Irwin et al. 10737* (MO, US); ca. 5 km N of jct. rd. W to Pires do Rio by BR 050, *Kral et al. 75939* (MO).

12. Paspalum heterotrichon Trinius, Sp. Gram. 3: pl. 285. 1829–1830. TYPE: Brazil. Without locality, *G. H. von Langsdorff 1829* (holotype, LE!; isotype, K! photo, SI!, US-2855297!). Figures 15, 16.

Paspalum gracile Schltdl., Linnaea 26: 134. 1854, hom. illeg. TYPE: Venezuela. Silla de Caracas, *Wagener 397* (not seen).

Paspalum heterotrichon Trin. var. *paucispicatum* Hack., Notizbl. Bot. Gard. Berlin-Dahlem 1(8): 328. 1897. TYPE: Haiti. Monte Furcy, 1896, *Picarda 1525* (holotype, W not seen; isotype, US-2855298!).

Paspalum ceresioides Carrillo, Revista Fac. Ci. Univ. Nac. S. Antonio 2: 145. 1968. Syn. nov. TYPE: Peru. Cuzco: Prov. Convención Chavuares, 920 m, 14 Abr. 1966, *C. Vargas C. 17215* (holotype, CUZ not seen; isotype, US!).

Caespitose, short-rhizomatous perennial, cataphylls pilose; culms (27–)45–90 cm tall, 1–1.9 mm diam., branching at the upper nodes or unbranched; internodes 2–3 cm long on the lower third and 6–12 cm long on the upper portion of the culms, terete, hollow, glabrous; nodes glabrous or pilose, with hairs white, 1–1.5 mm long. Sheaths (3–)5–12 cm long, glabrous or with the upper margins pilose. Ligules 0.5 mm long, membranous, truncate; pseudoligule present, a ring of hairs 3–4 mm long. Blades linear to linear-lanceolate, (4–)5–15 cm long, 1.5–4 mm wide, the abaxial surface glabrous, the adaxial one glabrous to sparsely pilose, the margins scabrous, attenuate, the apex acute. Peduncles (6–)10–16 cm long, terete, pilose. Terminal inflorescences 6–12 cm long, 2–2.5 cm wide; main axis (1–)2–4 cm long, 0.5 mm diam., pilose; racemes (1 to 2)3 to 7, (2–)3.5–6.5 cm long, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 3.5–4 mm wide, acuminate, glabrous, green at the middle portion and ferruginous at the wings, wings nerveless; pedicels 0.4 mm long, hispid, laterally inserted in the spikelets; spikelets solitary, arranged in 2 series. Spikelets ellipsoid, 2.3–3 mm long, 1–1.2 mm wide, pilose, upper glume and lower lemma subequal, with an annular thickening at the base. Upper glume as long as the spikelet, hyaline, acuminate, 3-nerved, with basal hairs ½ the length of the spikelet and papillose-pilose hairs at the margins, up to 3 mm long. Lower lemma membranous, acuminate, 3-nerved, with long hairs at the upper margins, otherwise glabrous. Upper anthecium ellipsoid, 1.5–1.8 mm long, 0.5 mm wide, glabrous, papyraceous; upper lemma with a tuft of macrohairs at the apex, and bicellular microhairs and silica bodies all over the surface; upper palea with prickles and silica bodies on the upper portion; lodicules 2, 0.1 mm long, rounded at the apex; stamens 3, anthers 1.2 mm long; stigma plumose. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 18, fig. 2. 1929. Swallen, Ann. Missouri Bot. Gard. 30: 93, fig. 18. 1943. Rodríguez, Ernstia 8(2–3): 38. 1998.

Distribution and habitat. *Paspalum heterotrichon* grows in Mexico, Central America (Honduras and Panama), and the Caribbean (Haiti and the Dominican Republic); in South America it is found in Colombia, Venezuela, Peru, and central Brazil, usually in open fields on limestone or rocky soils, between 300 and 2550 m elevation.

Paspalum heterotrichon shares with *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis* ellipsoid spikelets, thickened at the base, upper glume hyaline, and rachis of the racemes winged. *Paspalum petrense* differs by the long-acuminate spikelets and lower lemma with a similar pilosity pattern of the upper glume, i.e., with long hairs at the base of the surface and the margins. *Paspalum trachycoleon* is distinguished by the paired spikelets, while *P. phyllorhachis* has glabrous spikelets.

The specimen *Macedo 1121*, probably a poorly developed plant, presents smaller spikelets than typical, 1.7–2 mm long, and culms 25–30 cm tall.

Internodes are occasionally markedly branching, 3 cm long and thinner, up to 0.6 mm in diameter.

In P and US (2855297) there is a specimen, *Riedel s.n.*, that probably belongs to the type collection of *P. heterotrichon* (see Renvoize, 1978, for comments on *Langsdorff* and *Riedel* collections).

Representative specimens. BRAZIL. **Distrito Federal:** Reserva Ecológica do IBGE, *Oliveira 719* (SI). **Goiás:** without locality, *Glaziou 22576* (G, K, P, W). **Mato Grosso:** Cuiabá, *Malme 1562b* (US). **Minas Gerais:** Mun. Itubitaba, *Macedo 1121* (MO). **Without state:** without locality, *Riedel 966* (G, SI), *s.n.* (P, US-2855297). COLOMBIA. **Magdalena:** Santa Marta, *Smith 143* (BM, COL, G, MO, P). DOMINICAN REPUBLIC. **Azua:** San Juan, Loma La Vieja, Cordillera Central, *Ekman 13404* (US). **Santo Domingo:** Cordillera Central, Prov. de la Vega, Costanza, Bajo de La Angostura, *Ekman 14018*

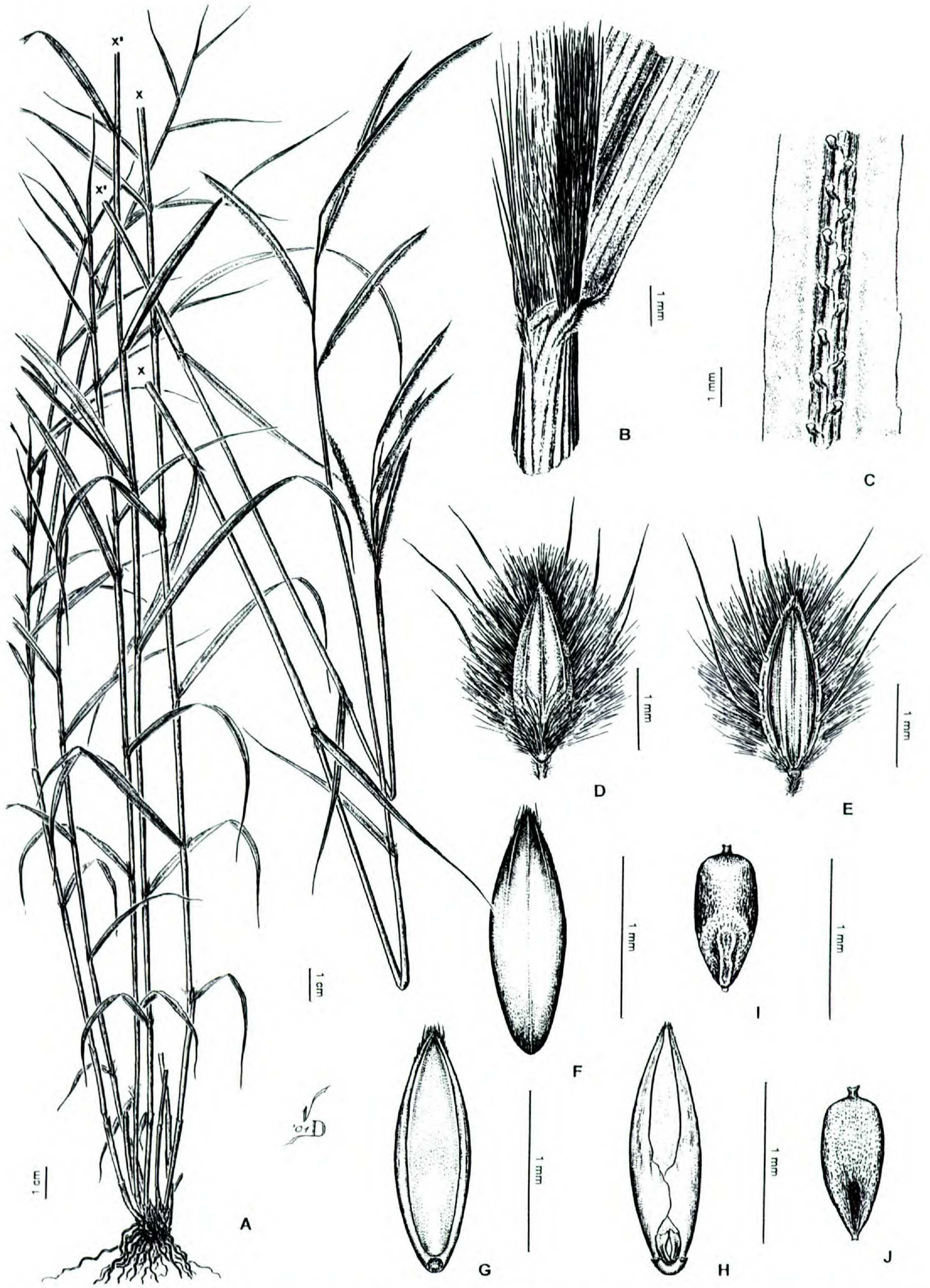

Figure 15. *Paspalum heterotrichon.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea with lodicules. —I. Caryopsis, scutellar view. —J. Caryopsis, hilum view. (A, B, D–J based on *Malme 1562b*, US; C based on *Tovar 4176*, US.)

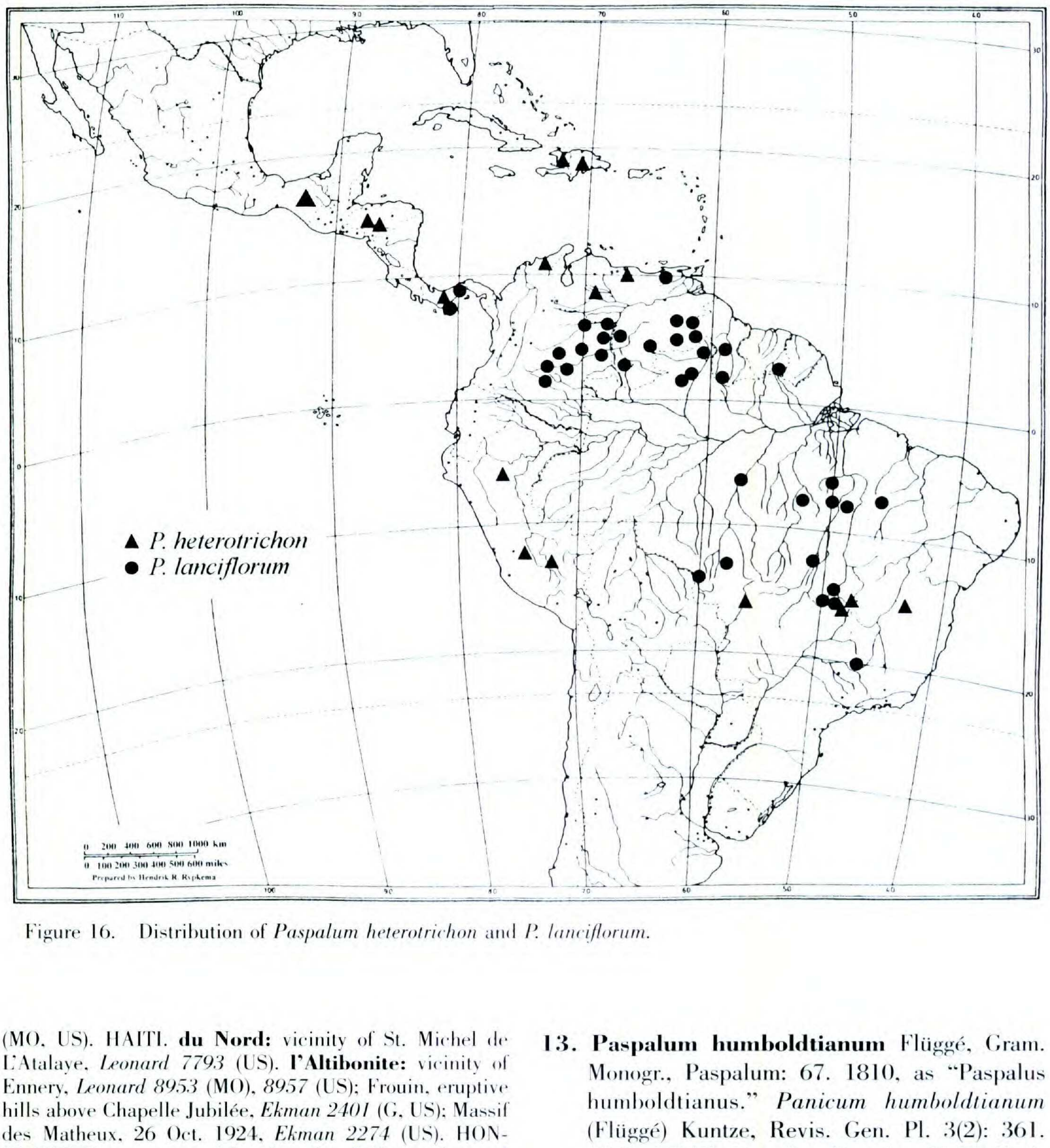
▲ P. heterotrichon
● P. lanciflorum
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 16. Distribution of *Paspalum heterotrichon* and *P. lanciflorum*.

(MO, US). HAITI. **du Nord:** vicinity of St. Michel de L'Atalaye, *Leonard 7793* (US). **l'Altibonite:** vicinity of Ennery, *Leonard 8953* (MO), *8957* (US); Frouin, eruptive hills above Chapelle Jubilée, *Ekman 2401* (G, US); Massif des Matheux, 26 Oct. 1924, *Ekman 2274* (US). HONDURAS. **Comayagua:** 4 km from San Isidro on the road to Pane, S side of rio Lima Gorge, *Moran 5505* (MO). **El Paraíso:** near km 2, road to Yuscarán, 5 Nov. 1951, *Swallen 11354* (MEXU, MO, US). **Francisco Morazán:** region of Las Mesas, *Swallen 10810* (MO, US), *11401* (US). MEXICO. **Chiapas:** El Pozo to Oxchuc, *Hernández Xolocotzi X-623* (US); Mun. Villa Corzo, above Colonia Vicente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54596* (MEXU, US). PANAMA. **Chiriquí:** near El Boquete, *Hitchcock 8297* (SI, US). PERU. **Amazonas:** Luya Province, Camporedondo, Fundo Cedro, 2450–2550 m, 24 Mayo 1989, *Días et al. 3493* (MO). **Huancavelica:** Huancavelica, Distrito de Huachocolpa, entre Marcavalle y Quintabamba, *Tovar 4176* (US). VENEZUELA. **Aragua:** 12 km S of Alto de Choroní along road to Maracay, *Davidse 3082* (K, MO); prope Colonia Tovar, *Fendler 1698* (G, K). **Lara:** Distr. Palavecino, Quebrada La Mata, towards the E side of the Parque Nac. Terepaima, *Burandt & Gantaume V0530* (MO).

13. Paspalum humboldtianum Flüggé, Gram. Monogr., Paspalum: 67. 1810, as "Paspalus humboldtianus." *Panicum humboldtianum* (Flüggé) Kuntze, Revis. Gen. Pl. 3(2): 361. 1898. TYPE: Ecuador: Puembo, *F. W. H. A. von Humboldt & A. J. A. Bonpland 3104* (holotype, B-W! photo, SI!; isotypes, BM!, P!, US-601340! photo, SI!). Figures 14, 17.

Paspalum distichophyllum Kunth, in H.B.K., Nov. Gen. Sp. 1: 86. 1816. TYPE: Colombia: Mesa de Cuello et Ibagué, Oct., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P!; isotypes, B!, US-2855276!).

Paspalum ciliatum Kunth, in H.B.K., Nov. Gen. Sp. 1: 87, pl. 24. 1816, hom. illeg. *Paspalum blepharophorum* Roem. & Schult., Syst. Veg. 2: 292. 1817. TYPE: Colombia: Ibagué y Valle de Caravajal, Monte Quindiu, Oct., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P!; isotypes, B!, US-2855275!).

Panicum obtectum J. Presl, Reliq. Haenk. 1: 301. 1830. *Tricholaena obtecta* (J. Presl) E. Fourn. ex Hemsl.,

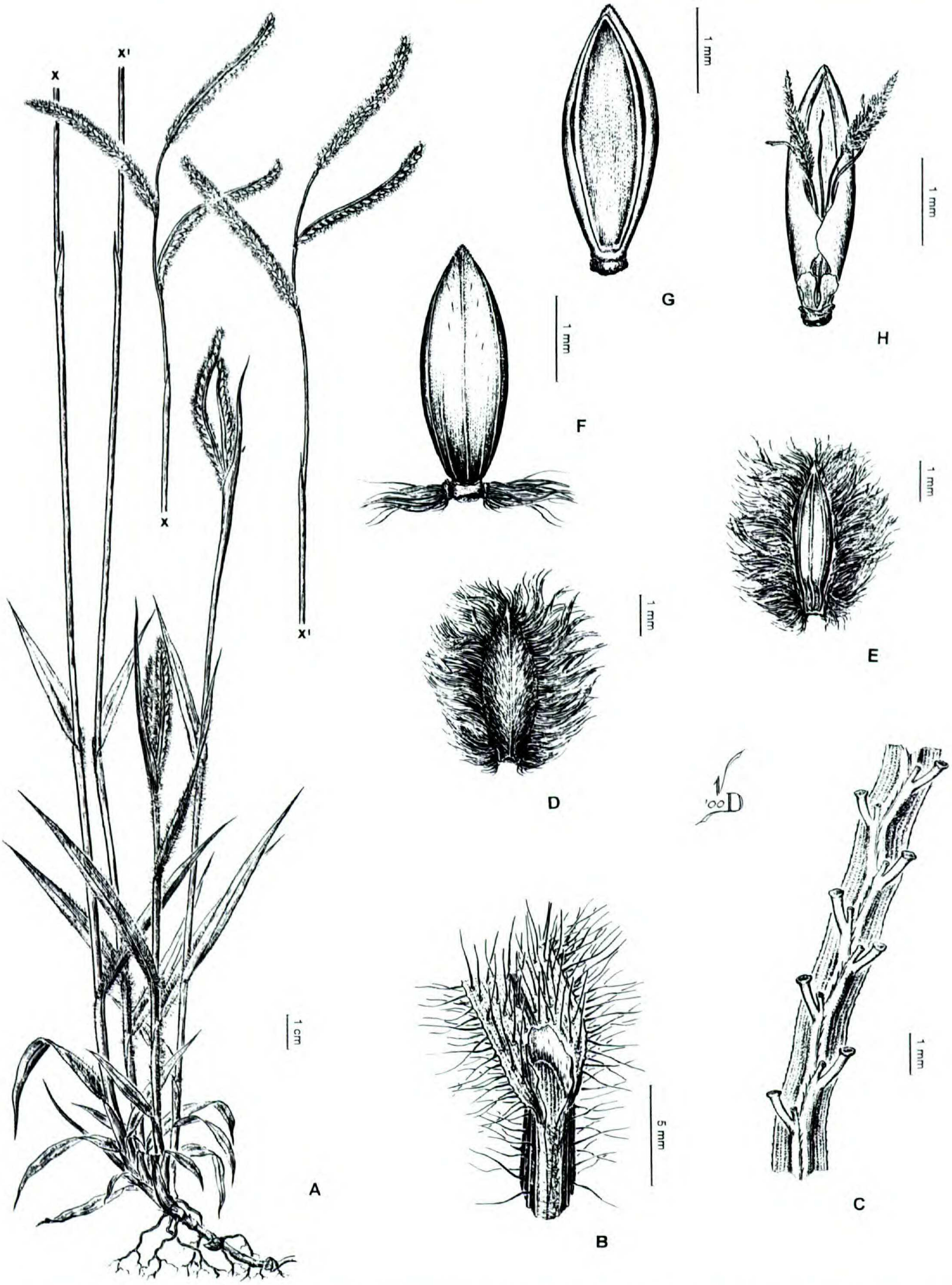

Figure 17. *Paspalum humboldtianum.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and gynoecium. (Based on *Zuloaga et al. 5887*, SI.)

Biol. Centr.-Amer., Bot. 3: 493. 1885, comb. illeg. *Tricholaena obtecta* (J. Presl) E. Fourn., Mexic. Pl. 2: 35. 1886. TYPE: Mexico. Without locality, *T. P. X. Haenke s.n.* (holotype, PR not seen; isotypes, US-2942536!, W).

Paspalum stuckertii Hack., in Stuck., Anales Mus. Nac. Buenos Aires 11: 63. 1904. *Paspalum humboldtianum* Flüggé var. *stuckertii* (Hack.) Hack., Allg. Bot. Z. Syst. 12: 97. 1906. TYPE: Argentina. Córdoba: Dpto. Punilla, Sierra Chica de Córdoba, en la punta de la Quebrada del Salto, del Ayo. Ochoa, 1000 m, 3 Apr. 1903, *T. J. V. Stuckert 13023* (holotype, W!; isotypes, BAA!, CORD!, G!, MO, US-80012! photo, SI!, US-557978!).

Paspalum soboliferum Chase, Contr. U.S. Natl. Herb. 24: 443. 1927. Syn. nov. TYPE: Ecuador. Loja: between Loja and San Lucas, 2100 m, 6 Sep. 1923, *A. S. Hitchcock 21495* (holotype, US-1164798! photo, SI!; isotype, S not seen).

Paspalum humboldtianum Flüggé var. *elegantissima* Beetle, Phytologia 52: 15. 1982. Syn. nov. TYPE: Mexico. Jalisco: 9 km from Los Volcanos, San José de Las Andrade, 29 Sep. 1980, *A. A. Beetle M-5962* (holotype, not located).

Short rhizomatous perennial, with leafy rhizomes; culms (30–)50–100 cm tall, 0.2–0.3 cm diam., erect or decumbent, lignified at the base, branching at the lower and middle nodes or unbranched; lower internodes 0.5–1 cm long, the upper ones 4–15 cm long, terete, hollow, glabrous or shortly pilose at the distal portion; nodes glabrous to pilose. Sheaths 4–11 cm long, longer than the internodes, overlapping, densely to sparsely papillose-pilose, with caducous tuberculate hairs at the upper portion, the margins ciliate. Ligules 1.2–2.5 mm long, membranous, brown, glabrous; pseudoligule absent; collar glabrous or pilose. Blades lanceolate, 5–21 cm long, 0.5–1.8 cm wide, flat, herbaceous, glabrous to sparsely pilose or hirsute, with long, tuberculate, caducous hairs, green to glaucous, shortly pseudopetiolate, the apex subulate. Peduncles exserted, up to 30 cm long, terete, glabrous. Terminal inflorescences exserted, 8–12 cm long, 3–5 cm wide; main axis 2–7 cm long, flat, with longitudinal nerves on the wings, scaberulous; racemes 2 to 6, ascendent, alternate and distant, slightly divergent from the main axis, ending in a naked point, occasionally in a spikelet; pulvini with a long tuft of white, rigid hairs; rachis of the racemes (3–)5–9 cm long, 1.2–1.5 mm wide, flat, shortly winged, green to purple, glabrous, scaberulous on the margins; pedicels unequal, up to 1.2 mm long, scaberulous; spikelets paired, and imbricate in 4 series, occasionally the lower spikelet aborted. Spikelets long-ellipsoid, 3–4 mm long, 1.2–1.4 mm wide, acute, plano-convex, pale or tinged with purple, the margins with long hairs; upper glume and lower lemma as long as the spikelet. Upper glume 3-nerved, hyaline, with plicate, corky margins covered with rigid, radiate and tuberculate hairs, 2–3.2 mm long, the rest of the surface sparsely pilose. Lower lemma 3-nerved, membranous, glabrous, scaberulous at the upper portion, depressed at the base. Upper anthecium ellipsoid, 2.6–3.2 mm long, 1–1.2 mm wide, membranous, pale, shiny, 0.4–0.6 mm shorter than the upper glume and the lower lemma; upper lemma 5-nerved, finely papillose with silica bodies, bicellular microhairs and prickles at the apex; upper palea papillose, with bicellular microhairs at the distal portion; lodicules 2, 0.6 mm long, truncate, conduplicate; stamens 3, anthers 1.6 mm long. Caryopsis not seen.

Common name. "Canutillo" (Venezuela).

Chromosome number. n = 10 (Hunziker et al., 1998); n = 20 (Saura, 1948); $2n = 40$ (Tateoka, 1962).

Distribution and habitat. Found from Mexico and Central America to Bolivia and central and northwestern Argentina. It grows on mountain slopes, on loose, rocky to sandy soils; it is also common at margins of highways and in forest edges or modified areas, between 400 and 2900 m elevation.

Paspalum humboldtianum is related to *P. polyphyllum* and *P. buchtienii* by the upper glume with corky margins and covered with radiate hairs, the rachis usually ending in a spikelet. *Paspalum polyphyllum* differs by the narrow (0.1–0.6 cm wide), not pseudopetiolate, linear to linear-lanceolate blades, rachis pilose and with anastomosed veins, spikelets with the upper glume with unequal marginal hairs, and lower lemma pilose on the distal margins and the upper portion of the surface. Differences with *P. buchtienii* were summarized in the treatment of the latter species.

Paspalum humboldtianum usually has spikelets tinged with purple and anthers purple or dark brown; however, pale spikelets and anthers were observed in several specimens, such as *Zuloaga et al. 5885*.

The type material of *P. humboldtianum* var. *elegantissima* was not located; it should be mentioned that no herbarium was cited by Beetle (1980) when describing the species. However, the diagnosis allowed us to conclude that this variety is a synonym of *P. humboldtianum*.

When describing *P. soboliferum* based on a single collection from Ecuador, Chase (1927) distinguished the species from *P. humboldtianum* mainly by the shorter, more slender, and ascending racemes, spikelets 2.8–2.9 mm long, with short hairs toward the margins. Therefore, we considered the type collection a poorly developed plant and placed *P. soboliferum* as a synonym of *P. humboldtianum*.

Spikelets with proliferous bracts were observed in several specimens from Mexico, such as *Müller 2036*, *Arséne 2813*, and *Schaffner 136*.

Representative specimens. ARGENTINA. **Catamarca:** Dpto. Andalgalá, Las Payvas, *Joergensen 1765* (LIL, MO, SI, US). **Córdoba:** Ascochinga, *Burkart 10211* (SI); Dpto. Punilla, Sierra Chica, *Stuckert 14159* (CORD, G, MO, SI). **Jujuy:** Río Perico, *Burkart & Troncoso 11014* (SI); Dpto. Tumbaya: Volcán, *Zuloaga et al. 5885* (SI). **La Rioja:** Velazco, *Soriano 986* (SI). **Salta:** Dpto. Capital, San Luis, *Filipovich 398* (LIL); Dpto. Candelaria, Cuesta de Muquillo, *Schreiter 9251* (LIL, MO, US). **San Luis:** Dpto. Gral. Pedernera, San José del Morro, Ea. La Morena, *Boelcke & Moore 16646* (SI). **Tucumán:** Tafí del Valle, *Burkart 5335* (SI); Dpto. Burruyacú, camino a Cerro Medina, *Villa Carenzo et al. 1818* (LIL). BOLIVIA. **Chuquisaca:** Sucre by the exit to Tarabuco, *Wood 7852* (US). **Cochabamba:** Morochata, *Cárdenas 3410* (LIL); W of Cochabamba, *Hitchcock 22830* (US). **La Paz:** viciniis Sorata, *Mandon 1254* (BM, G, P, US, W). **Santa Cruz:** 10 km E of Samaipa, *Renvoize & Cope 4038* (MO); Buena Vista, *Steinbach 6618* (BM, G, US). **Sucre:** Sucre, *Cárdenas 515* (US). **Tarija:** Camargo, *Fiebrig 3082* (G, LIL, SI, W). COLOMBIA. **Antioquia:** San Jerónimo, *Archer 629* (MA, US). **Boyacá:** without locality, *Saravia 4006* (COL). **Cauca:** Chisquío, Finca Los Derrumbos, *Asplund 10498* (G, US). **Cundinamarca:** La Esperanza, *Cuatrecasas 3001* (MA). **Huila:** 6 km SE of Altamira along road to Florencia, *Davidse et al. 5597* (COL, MO). **Norte de Santander:** vicinity of Pamplona, *Killip & Smith 19770* (US). **Providencia:** Pico-casabaja, *Idrobo 11636* (COL). **Santander:** Zapatoca, *Fassett 25502* (COL, US). **Without departament:** without locality, *Mutis 5537* (US). **Tolima:** Valle de San Juan, Cerro del Real Mina del Sapo, *Echeverry 1251* (COL). **Valle:** near Sevilla, *Barclay & Juajibioy 5703* (MO, US); Cordillera Occidental, E slope, Cali, Loma Los Cristales, *Cuatrecasas et al. 25702* (COL, US). COSTA RICA. **Cartago:** San Juan Norte, *Pohl et al. 11434* (US). **Guanacaste:** 2 km E of Liberia, *Pohl et al. 11327* (US). ECUADOR. **Azuay:** vicinity of Cuenca, along Río Milchichi, about 5 km N of Cuenca, *Camp E-2743* (G, US). **Chimborazo:** Chunchi-Alausi, *Acosta Solís 21454* (US). **Loja:** halfway between Loja and Catamayo, *Grignon 84257* (MO). **Oro:** between Portovelo and El Tambo, *Hitchcock 21306* (US). **Pichincha:** Tumbaco, *Asplund 6531* (G, P, US). **Tungurágua:** Ambato, *Hitchcock 21710* (US); Baños, *Asplund 7593* (G, P, US). EL SALVADOR. **Ahuachapán:** P.N. El Imposible, *Sermeño s.n.* (MO). **San Salvador:** San Salvador, *Calderón 1152* (US). GUATEMALA. **Alta Verapaz:** 5 mi. S of Cobán along Hwy. CA 14, *Thomas s.n.* (MO). **Santa Rosa:** Cerro Redondo, *Heyde & Luz 6271* (G). **Sololá:** Volcán San Pedro, *Steyermark 477177* (US). HONDURAS. **Francisco Morazán:** vicinity of El Zamorano, *Swallen 10776* (US). **Olancho:** Mun. La Unión, 5 mi. E of La Unión along road to Olanchito, *Davidse et al. 35448* (MO). MEXICO. **Chiapas:** 22 km NE of Motozintla on hwy. to Amatenango, *Stevens & Martínez 25701* (SI). **Colima:** Alzada, *Hitchcock 7055* (US). **Guanajuato:** ca. 8 km W of San Felipe on Cerro del Fraile, *Sohns 427* (US). **Guerrero:** Montes de Oca, Vallecitos, *Hinton 11400* (US). **Jalisco:** Mun. Tlajomulco de Zuñiga, Cerro Viejo region, 35–40 km due SSW of Guadalajara, *Machuca Nuñez 4640* (MO). **Michoacán:** Mun. Apatzingan, *Leavenworth & Leavenworth 1649* (US). **Morelos:** Cuernavaca, *Hitchcock 6837* (US). **Nayarit:** La Yesca, 23 km al SE de Puente de Camotlán, *Tenorio & Flores 16710* (MO). **Oaxaca:** Dist. Yautepec, Mun. Santa María Ecatepec, desviación a San Matías y Santa María Zapotitlán, *Flores Flanco et al. 3643* (MO). **San Luis Potosí:** 3 mi. SW of San Luis Potosí, *Reeder et al. 3313* (US). **Sonora:** Tepopa, Sierra Saguaribo, *Gentry et al. 19307* (US). **Tamaulipas:** Mun. Villa de Casas, central part of the Sierra de Tamaulipas, *Martínez & Luyando F-1953B* (US). **Veracruz:** Zacuapán, *Purpus 2002* (US). **Zacatecas:** Mun. Valparaiso, 1 km al N de San Francisco, *Rzedowski 17636* (US). NICARAGUA. **Nueva Segovia:** Santa María de los Pinos, 5 km NE de Dipilto, *Stevens & Montiel 24761* (MO). PANAMA. **Chiriquí:** Alto Boquete, *Partch 69–91* (MO); roadside near El Hato del Volcán, *Stockwell & Aiello 893* (MO, SI). PERU. **Amazonas:** Prov. Chachapoyas, 5 km W of Chachapoyas on road to Caclic, *Hutchison & Wright 4495* (G, MO, P, US). **Apurimac:** Challhuanaca, Aymaraes, *Núñez 7175* (MO). **Ayacucho:** Chumbes, *Balls 6923* (BM, US). **Cajamarca:** Prov. Chota, Yamaluc, a 11 km sobre la carretera Cochabamba–Huambos, *Sánchez Vega 2341* (SI). **Cuzco:** Prov. Convención, Amaybamba, *Marin 851* (US). **Huancavelica:** entre Izcuchaca y Acoria, *Tovar 1005* (US). **Lambayeque:** Prov. Chiclayo, Cerro Reque, *Llatas Quiroz 2322* (MO). **Lima:** entre Lunahuaná y Cañete, *Ferreyra 5373* (US). VENEZUELA. **Aragua:** Distr. Ricaurte, ca. 10–12 km SW of Colonia Tovar along the Colonia Tovar–La Victoria Hwy., *Davidse & Miller 28159* (MO). **Distrito Federal:** 5.5 km down road to Carayaca, *Davidse & Tillett 4073* (MO). **Lara:** Distr. Jiménez, 4–5 km S of Sanare, 9°42'N, 69°38'W, *Davidse & González 21370* (MO). **Mérida:** Sebastopol, *Chase 12294* (US). **Miranda:** Los Teques, *Burkart 16984* (SI). **Táchira:** Mun. Andrés Bello, Loma Blanca, Aldea Salomón, *Tamayo 2281* (US).

14. **Paspalum imbricatum** Filgueiras, Bradea 3: 153, fig. 2. 1981. TYPE: Brazil. Mato Grosso: Mun. Sidrolândia, Rod. BR-163, orla de brejo, 27 Oct. 1970, *G. Hatschbach 25281* (holotype, US-2705820! photo, SI!). Figure 25.

Caespitose perennial; culms 1–1.5 m tall, 0.3–0.5 cm diam., herbaceous to rigid, erect, unbranched; internodes 15–30 cm long, slightly compressed, hollow, glabrous, pale or tinged with purple; nodes brown, glabrous. Sheaths 15–25 cm long, densely hirsute, with papillose-pilose hairs at the distal portion, glabrous at the base, the margins membranous, shiny on both surfaces. Ligules membranous, 1–1.5(–2) mm long, brown, glabrous; pseudoligule a ring of hairs up to 1.3 mm long. Blades linear-lanceolate, 35–60 cm long, 0.6–1 cm wide, acute, pungent, mostly basal, flat, rigid, ascendent, the basal ones long pseudopetiolate, densely hirsute, with tuberculate hairs, on both surfaces. Peduncles up to 40 cm long, terete, glabrous, pale or purple. Terminal inflorescences exserted, 10–15 cm long, 8 cm wide; main axis 1.5–5.5 cm long, flat; racemes (2)5 to 7(11), (5–)10–14(–16) cm long, ascendent, slightly divergent from the main axis, alternate, ending in a naked point; pulvini shortly pilose; rachis of the racemes 2.4–2.8(–3) mm wide, flat, the margins membranous to hyaline, nerveless, glabrous, green, shortly winged, wings purple; pedicels short; spikelets solitary, densely imbricate in 2 series. Spikelets broadly ovoid, 5–5.5 mm long, 2.8–3 mm wide, plano-convex, glabrous, pale, upper glume and lower lemma subequal, or the lower lemma slightly longer, cordate, the apex acute to almost rounded, the margins winged. Upper glume papyraceous, corrugate in the lower half, 5-nerved with 3 central nerves reaching the apex. Lower lemma glumiform, 5-nerved, corrugate in the lower half. Upper anthecium long-ellipsoid, 3.8–4 mm long, 1.2 mm wide, plano-convex, membranous, pale, pilose toward the apex, finely papillose; upper lemma with small papillae evenly distributed all over the surface, with macrohairs and bicellular microhairs at the apex, hispidulous toward the margins and in the lower portion; upper palea hispidulous toward the apex; lodicules 2, ca. 0.4 mm long, conduplicate, hyaline; stamens 3, anthers 2–2.5 mm long; stigmas 2, plumose, lateral. Caryopsis not seen.

Distribution and habitat. Endemic to Brazil, where it is found in cerrados in the Distrito Federal and the states of Mato Grosso and Goiás, between 950 and 1250 m elevation.

Paspalum imbricatum is a member of section *Pectinata*, sharing cordate upper glume and lower lemma, the margins winged; it is easily distinguished by the glabrous spikelets.

15. Paspalum lanciflorum Trinius, Sp. Gram. 3: pl. 286. 1829–1830. TYPE: Brazil. Mato Grosso: Cuiabá, 1829, *G. H. von Langsdorff s.n.* (holotype, LE!; isotype, US-80075!). Figure 16.

Paspalum contractum Pilg., Bot. Jahrb. Syst. 25: 709. 1898. TYPE: Colombia. Meta: Los Llanos de San Martín, Ago. 1868, *M. A. Stübel 190a* (holotype, B!; isotype, US-2942134!).

Paspalum echinotrichum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 9. 1921. TYPE: Brazil. Roraima: Rio Branco, Surumú, Sep. 1909, *E. H. G. Ule 8033* (lectotype, designated by Judziewicz (1990: 485), B!; isolectotypes, K!, US-2854675! photo, US).

Paspalum piligerum Swallen, Fieldiana, Bot. 28: 24, fig. 2. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kun and Uaduara–Paru, in valley of Rio Kukenan, S of Mount Roraima, 1065–1220 m, 1 Oct. 1944, *J. A. Steyermark 59090* (holotype, US-1911660!; isotype, F!).

Paspalum aureolatum Swallen, Fieldiana, Bot. 28: 22, fig. 1. 1951. TYPE: Venezuela. Territorio Federal Amazonas: summit of Cerro Duida, 1025–1200 m, 2 Sep. 1944, *J. A. Steyermark 58234* (holotype, US-1911652! photo, SI!).

Caespitose, shortly rhizomatous perennial; culms 45–120 cm tall, erect, unbranched; internodes 9–14 cm long, glabrous, brown; nodes glabrous to pilose, brown, compressed. Sheaths 9–17 cm long, densely hirsute on the distal portion, otherwise sparsely pilose or glabrescent, the adaxial surface shiny, brown. Ligules membranous, 1.5–3.2 mm long, glabrous, brown; pseudoligule a ring of hairs up to 0.8 cm long. Blades linear-lanceolate, 7–35 cm long, (0.3–)0.5–1(–1.5) cm wide, flat or with involute margins, densely papillose-pilose, with tuberculate hairs up to 7 mm long, the midnerve conspicuous on the adaxial surface. Peduncles long-exserted, up to 40 cm long, terete, glabrous. Terminal inflorescences subdigitate, yellow, occasionally with a papyraceous bract, up to 4 mm long, at the base; main axis absent or up to 1.5 cm long, glabrous, flat; pulvini pilose; racemes (1)3 to 6(11), ascendent, 5–15 cm long, subconjugate and ending in a naked point; rachis of the racemes (4–)5–7 mm wide, winged, green at the center, the midnerve white, with purple, membranous and glabrous margins; pedicels short, glabrous, flat; spikelets solitary, imbricate in 2 series. Spikelets long-ovoid, (4.8–)5.6–7.2 mm long, 1.2–2.5 mm wide, plano-convex, acuminate, pale, pilose. Upper glume as long as the spikelet, membranous, rounded and densely pilose at the base, the basal margins pilose, with hairs up to 2 mm long, otherwise glabrous, 3-nerved. Lower lemma slightly shorter than the upper glume, lanceolate, 3-nerved, densely pilose at the basal margins, the median portion with conspicuous, tuberculate hairs 2.5–3 mm long. Upper anthecium ovoid, 3.2–4.7 mm long, 0.9–2 mm wide, membranous, pale, stipitate, the stipe 0.3 mm long; upper lemma finely papillose, with bicellular microhairs and silica bodies at the apex, otherwise glabrous; lodicules 2, ca. 0.4 mm long, conduplicate; stamens 3, anthers 1.6 mm long; stigma lateral. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 26, fig. 7. 1929 (under *P. contractum*). Judziewicz, Fl. Guianas: 469, fig. 83, E. 1990.

Common name. "Pama" (Venezuela).

Distribution and habitat. Panama, Colombia, Guyana, Surinam, Venezuela, Brazil (Roraima, Pará, Maranhão, Mato Grosso, Minas Gerais, Goiás, and Distrito Federal), and Bolivia; it grows in savannas subjected to fire, on limestone, sandy, or rocky soils, between sea level and 1200 m.

Paspalum lanciflorum belongs to section *Pectinata*; within this section it is related to *P. cachim-*

boense, which differs by the annual habit, with branched, geniculate culms, rachis of the racemes 2–3 mm wide, spikelets 4–4.3 mm long, and upper anthecium 2.2–2.5 mm long. Also, *P. lanciflorum* is distinguished from *P. pectinatum* and *P. cordatum* by the glume densely pilose on the lower portion, not cordate, and upper anthecium stipitate, ⅓–½ the length of the spikelet.

This species is quite variable in its overall morphology. The specimens *Wurdack & Guppy 27*, *Tate 157*, and *Hahn et al. 5592b* are approximately 40–50 cm tall, with all blades basal. On the other hand, *Kuhlmann 1674*, *Glaziou 20084*, *22544*, and *Zuloaga et al. 4413* are more robust specimens, ca. 120 cm tall, with blades evenly distributed along the culms. It is noteworthy to mention the presence of densely papillose-pilose specimens, e.g., *Zuloaga et al. 4413*, *Tamayo s.n.*, *Egler & Raimundo 1262*, and others, as sparsely pilose, such as *Williams 13088* and *Maguire et al. 32038*.

Three to six racemes per inflorescence are frequent in this species; nevertheless, one to three racemes are found in *Swallen 4029*, *Williams 13088*, *Wurdack & Guppy 27*, *Gifford G-101*, *Oliveira & da Silva 700*, *Tamayo 3198*, *Ramirez 961*, and *Heringer et al. 4615*; the specimen *Echeverry et al. 2312* has 11 racemes per inflorescence.

Spikelets are small, 4.8–5 mm long, 1.7–2 mm wide in *Davidse et al. 22647* and *Blydenstein 1468*.

Chase (ined.) distinguished *P. contractum* from *P. lanciflorum* by the number of racemes (1 to 3 vs. 3 to 6) and the relative length of the lower lemma (as long as the spikelet vs. shorter than the spikelet). Our analysis of herbarium material did not allow us to distinguish between both taxa.

According to Judziewicz (1990), the specimen *Pohl 1454* (seen in B and W) is a syntype of the species; nevertheless, we examined at LE a specimen collected by *von Langsdorff* (see type material), and there are no elements that suggest Trinius had cited two syntypes when describing the species.

Representative specimens. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parque Nacional Noel Kempff Mercado, Campamento Las Gamas, *Killeen et al. 4929* (MO). BRAZIL. **Distrito Federal:** Brasília, Bacia do Rio S. Bartolomeu, *Heringer et al. 4615* (US); Serra de Arruda, *Glaziou 22544* (K, P, US); Serra Dourada, *Pohl 1454* (G). **Goiás:** Mun. Couto Magalhaes, 16 km W of Piqizeiro along GO-70, *Plowman et al. 19132* (US). **Maranhão:** Balsas, Morro antes do Rio Tem, *Oliveira & da Silva 700* (SI); Carolina to San Antonio de Balsas, *Swallen 4029* (US). **Mato Grosso:** ca. 270 km N de Xavantina, *Gifford G-101* (US); entre Barão de Capanema e Utiarity, *Kuhlmann 1674* (US). **Minas Gerais:** Ribeirão Taquarucu, *Glaziou 20084* (BM, K, P, US). **Pará:** Tapajós, Rio Cururú, *Egler & Raimundo 1262* (US). **Roraima:** Aldeia Tucham Paulo, para a base do Roraima, *Rondon s.n.* (US-2454780); Mt. Roraima, Paulo, *Tate 157* (US). COLOMBIA. Cravo Norte Arauca, al S del Río Meta, *Blydenstein 1468* (US). **Meta:** 13 km O de La Macarena, vía a Conejos, *Callejas & Marulanda 6886* (SI); carretera de Bella Vista a Piñalito, *Echeverry & Jaramillo 2312* (COL). **Vichada:** Mun. Puerto Carreño, Base Terecay, *Amat & Castillo 3* (COL). GUYANA. Potaro-Siparumi Region, Kato, *Hahn et al. 5592b* (US); Annai Hillside, *Goodland 923* (US). PANAMA. **Herrera:** ca. 7 mi. SW of Las Minas, *D'Arcy & Antonio 13527* (MO). SURINAM. Sipaliwini savana area on Brazilian frontier, *Oldenburger et al. 5* (US). VENEZUELA. **Amazonas:** Canaima, R. Carrao, *García Barriga 21426* (COL); Santa Bárbara savanna, junction of Ríos Ventuari and Orinoco, *Maguire et al. 32038* (US); alrededor del bajo Río Cataniapo, Pto. Ayacucho, *Williams 13088* (US). **Anzoátegui:** Dist. Bolívar, S of El Zamuro, Fila El Purgatorio, *Davidse & González 19314* (MO). **Bolívar:** El Pauji, *Liesner 19350* (SI); pié de la Roca to Guayaraca, *Davidse & Huber 22647* (MO); Gran Sabana, Vía Kavanayen, El Jardín, *Ramírez 961* (MO); Hato Santa Teresa, *Tamayo 3198* (MO); Hato La Vergareña, *Wurdack & Guppy 27* (US); 5 km al S de San Ignacio de Yuruaní, Gran Sabana, *Zuloaga et al. 4413* (K, SI, US).

16. Paspalum longiaristatum Davidse & Filgueiras, Novon 3: 129, fig. 1. 1993. TYPE: Brazil. Goiás: Mun. Niquelândia, Macedo, 14°18′S, 48°23′W, 13 Apr. 1992. *T. S. Filgueiras 2277* (holotype, IBGE!; isotypes, B not seen, BM!, FLAS not seen, ICN!, ISC not seen, K!, MEXU-62.8764!, MO!, NY not seen, P not seen, SI!, SP not seen, R not seen, RB not seen, UB not seen, UFG not seen, US not seen). Figure 23.

Caespitose annual; floriferous culms 15–36 cm tall, 0.8–1 mm diam., branching at the lower nodes; internodes terete, hollow, glabrous; nodes dark, pilose. Sheaths 3–7 cm long, papillose-pilose, the margins smooth. Ligules membranous-ciliate, the membranous portion 0.5–0.8 mm long, cilia 0.2–0.8 mm long. Blades linear, 3.5–8.2 cm long, 1–2 mm wide, attenuate at the base, papillose-pilose on both surfaces, more densely so toward the base. Peduncles terete, 0.5 mm diam., glabrous or with papillose-pilose hairs. Terminal inflorescences exserted, 5–8 cm long; main axis 1–2.5 cm long, papillose-pilose, ending in a naked point; racemes 1 to 2(4), 2–7 cm long, alternate, arcuate, ascendent and divergent; pulvini pilose; rachis of the racemes membranous, 4–6 mm wide, winged, hyaline, and ciliate at the margins, the adaxial surface with papillose-pilose hairs, the abaxial surface glabrous; pedicels 0.1–0.2 mm long, hispid; spikelets solitary, imbricate in 2 series. Spikelets ellipsoid, 1.8–2.2 mm long, 0.5–0.6 mm wide, pilose, brown or tinged with purple, shiny. Upper glume hyaline, 3-nerved with one central and two marginal nerves, pilose at the base, the hairs reaching ½ the length of the spikelet, the margins pilose with ascendent hairs, awned, awn 6–12.2 mm long, scabrous. Lower lemma glumiform, slightly shorter than the upper glume, membranous, 3-nerved, awned, awn 0.3–2 mm long, scabrous. Upper anthecium ellipsoid, 1.5–1.8 mm long, 0.7–0.8 mm wide, membranous, shiny; upper lemma 5-nerved, with prickles, bicellular microhairs and silica bodies at the upper portion; upper palea 2-nerved; lodicules absent; stamens 3, anthers 1.4–1.8 mm long, purple at maturity; stigma plumose. Caryopsis 1–1.2 mm long, 0.4–0.5 mm wide; hilum punctiform, basal, embryo more than half the length of the caryopsis.

Distribution and habitat. Endemic to central Brazil, in the state of Goiás, where it is found in cerrados, in serpentine, rocky soils at 1000 m.

Paspalum longiaristatum differs from *P. biaristatum* by the perennial habit, spikelets 3.8–4.5 mm long, awn of the upper glume 4–7.1 mm long, and awn of the lower lemma 3.8–4.5 mm long of the latter taxon.

Representative specimens. BRAZIL. **Goiás:** Macedo, ca. 15 km N of Niquelândia, *Brooks et al. 144* (MO); Macedo, a 18 km de Niquelândia, *Filgueiras 2342* (K, MO, SI, US), *Filgueiras 2780* (MO, US), *Oliveira et al. 638* (US); km 23 ao 3 da estrada de terra a direita da mina de niquel, *Fonseça et al. 227* (MO, SI); Mun. Alto Paraiso, Vale da Lua, 14°10′S, 98°47′S, *Filgueiras & Oliveira 3292* (US).

17. Paspalum malmeanum Ekman, Ark. Bot. 10: 12, tab. 4, fig. 3. 1911. TYPE: Brazil. Mato Grosso: Santa Ana da Chapada, 31 May 1903, *G. O. A. Malme s.n.* (holotype, S not seen; isotype, US-80089!). Figure 23.

Caespitose, shortly rhizomatous perennial; culms 60–90 cm tall, few-noded; internodes 6–10 cm long, purple, terete, hollow, striate; nodes glabrous. Sheaths usually longer than the internodes, slightly compressed, glabrous, pale or tinged with purple, shiny, the margins ciliate or glabrous. Ligules membranous, 0.2 mm long, brown, glabrous; pseudoligule a ring of hairs up to 1.2 mm long. Blades linear, 10–45 cm long, 0.1 cm wide, involute, papillose on the adaxial surface, glabrous and smooth on the abaxial surface, the margins papillose-pilose toward the base with hairs up to 6 mm long, otherwise glabrous, the apex subulate. Peduncles exserted, terete, up to 35 cm long, glabrous. Terminal inflorescences exserted; main axis absent; pulvini with a tuft of short hairs and occasionally with 2 small bracts on the basal pulvini; racemes 2, conjugate, 7–14 cm long, occasionally with a single raceme present; rachis of the racemes 1.2–2 mm wide, ending in a naked point, purple or with the margins red-tinged, glabrous, the wings flat; pedicels subterete, glabrous to short pilose at the apex; spikelets solitary, densely imbricate in 2 series. Spikelets ellipsoid, 1.6–2 mm long, 0.8–1.2 mm wide, villous, early deciduous, upper glume and lower lemma subequal. Upper glume membranous, 3-nerved, the margins rigid, densely pilose at the basal portion with short and appressed, tuberculate hairs, the margins ciliate, silky with hairs up to 1.5 mm long, the rest of the surface glabrescent. Lower lemma glumiform, 3-nerved, pilose at the margins and ⅔ of the surface. Upper anthecium obovoid, 1.5 mm long, 0.8–1 mm wide, plano-convex, membranous, pale, shiny, rounded at the apex; upper lemma smooth; lodicules 2, 0.1 mm long, conduplicate; stamens 3, anthers 1 mm long. Caryopsis ellipsoid, 1 mm long; hilum punctiform, embryo less than ½ the length of the caryopsis.

Chromosome number. $2n = 20$ (Killeen, 1990).

Distribution and habitat. *Paspalum malmeanum* grows in Bolivia and Mato Grosso, Brazil, where it is usually found in flooded savannas on sandy soils between 0 and 500 m elevation.

Paspalum malmeanum is related to *P. eucomum*, which differs by the spikelets 2.5–3 mm long. Other features of its distribution and habitat are pointed out in the treatment of *P. eucomum*.

Representative specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff M., campamento Los Fierros, *Gutiérrez et al. 655* (MO); Ñuflo de Chávez, 3 km SW of Concepción on road around reservoir, *Killeen 2024* (G, LPB, MO, SI, US); Ñuflo de Chávez, Est. Las Madres, *Killeen 2076* (MO, SI, US); Ñuflo de Chávez, Estancia Santa María, *Killeen 2478* (MO, SI, US). BRAZIL. **Mato Grosso:** NW of São Lourenço, E of Rio Ibo, *Chase 11962* (MO, US); Juruena, *Kuhlmann 1667* (US); caminho da Guia Linha Telegrafica, *Kuhlmann 1668* (US).

18. Paspalum niquelandiae Filgueiras, Novon 5: 30, fig. 1. 1995. TYPE: Brazil. Goiás: Mun. Niquelãndia, ca. 14°18′S, 48°23′W, ca. 2 km este da localidad de Macedo, 19 May 1993, *T. S. Filgueiras & F. C. de A. Oliveira 2461* (holotype, IBGE!; isotypes, F not seen, G not seen, ICN not seen, K!, MEXU not seen, MG not seen, MO!, R not seen, SI!, SP not seen, US not seen). Figure 23.

Rhizomatous perennial; culms 120–185 cm tall, 0.4–0.6 cm diam., unbranched; internodes 5–8, glabrous, hollow; nodes glabrous, dark. Sheaths glabrous or pilose toward the base and papillose-hispid toward the distal portion, keeled, the margins ciliate or glabrous. Ligules 0.2–0.3 mm long, membranous; pseudoligule a ring of hairs 5–8 mm long. Leaf blades lanceolate, 20–45 cm long, 0.8–

2.2 cm wide, acuminate, flat, glabrous to papillose-hispid, the margins scabrous or ciliate. Peduncles exserted, 12–22 cm long, glabrous. Terminal inflorescences 14–18 cm long, 6–9 cm wide; main axis 9–15 cm long, glabrous, terete or wavy; racemes 8 to 30, 2.5–8.5 cm long, alternate, ascendent, ending in a naked point, occasionally in a spikelet; pulvini pilose, with 2–2.5 mm long hairs; rachis of the racemes 1–1.5 mm wide, foliaceous, flexuous toward the apex, glabrous or scabrous, midnerve manifest and wings with thin, longitudinal nerves; pedicels 0.1–0.3 mm long, scabrous; spikelets paired, arranged in 4 series. Spikelets ellipsoid to ovoid, 2.3–3.3 mm long, 1–1.4 mm wide, pilose, plano-convex. Upper glume membranous, 3-nerved, the margins corky, with radiate, tuberculate hairs 0.3–1 mm long, the rest of the surface glabrous or shortly hispid. Lower lemma flat, membranous, 3-nerved, glabrous, as long as the upper glume, depressed at the base. Upper anthecium ovoid, 2.2–2.7 mm long, 1–1.1 mm wide, membranous to chartaceous, glabrous; upper lemma 5-nerved, with simple papillae regularly distributed all over the surface and sparse bicellular microhairs; lodicules 2, 0.1–0.2 mm long; stamens 3, anthers 1.2–2 mm long; stigmas plumose. Caryopsis not seen.

Distribution and habitat. Endemic to the state of Goiás, Brazil, where it grows on outcrops of serpentine, rocky soils, near edges of gallery forests.

Paspalum niquelandiae is related to *P. burmanii* and *P. humboldtianum.* Differences with *P. burmanii* were summarized in the treatment of that species. In *Paspalum humboldtianum* plants are (30–)50–100 cm tall, with branched or unbranched culms, two to six racemes per inflorescence are present, and spikelets are long ellipsoid, with radiate hairs, 2–3.2 mm long, at the margins of the upper glume.

19. Paspalum pectinatum Nees ex Trinius, Sp. Gram. 1: pl. 117. 1828. *Paspalum pectinatum* Nees, Fl. Bras. Enum. Pl. 2: 34. 1829, hom. illeg. *Anastrophus pectinatus* (Nees ex Trin.) Schltdl. ex B. D. Jacks., Index Kew. 1: 118. 1893. TYPE: Brazil. Without locality, *F. Sellow s.n.* (holotype, LE not seen; isotypes, B!, G!, K! photo, SI!, LE not seen, US-2942525!, W!). Figures 18, 19.

Caespitose, shortly rhizomatous perennial; floriferous culms 35–100 cm tall, erect, few-noded; internodes 2 to 4, 7–14 cm long, 0.2 cm diam., hollow, slightly compressed, striate, glabrous; nodes glabrous, brown. Sheaths usually longer than the internodes, the basal ones shiny, red-tinged to brown, glabrous; upper sheaths green, keeled, villous to hirsute all over the surface or only toward the upper portion, the margins membranous. Ligules membranous, 0.3–0.5 mm long, brown, glabrous; pseudoligule a tuft of white hairs 3–4 mm long. Leaf blades linear, 10–30 cm long, 0.2–0.8 cm wide, mostly basal, flat or with involute margins, densely pilose on both surfaces, the base attenuate, the apex acute. Peduncles long-exserted, up to 30 cm long, finely striate, glabrous. Terminal inflorescences with 2(3 to 5) conjugated, ascendent racemes, 2–8 cm long; main axis absent or up to 1 cm long; pulvini shortly pilose; rachis of the racemes shortly winged, 2–2.5 mm wide, glabrous, membranous, green, with light-brown to purple, crenate, glabrous or pilose, margins, the midnerve manifest, ending in a naked point; pedicels up to 0.6 mm long, flat, glabrous; spikelets solitary, densely imbricate and arranged in 2 series. Spikelets lanceolate, 5–8 mm long, 2–3.3 mm wide, dorsiventrally compressed, slightly plano-convex, cordate, the apex acute, pilose, pale or tinged with purple. Upper glume as long as the spikelet, 3–5-nerved, winged, papyraceous to hyaline, cordate, slightly convex, glabrous, the base cordate, corrugated at the middle portion. Lower lemma 4.5–7.2 mm long, 3-nerved, not winged, sparsely pilose, subcordate, the margins papillose-pilose with rigid, tuberculate hairs 1–2.5 mm long. Upper anthecium ellipsoid, 4–5 mm long, 1.4–1.6 mm wide, plano-convex, papyraceous, pale; upper lemma finely papillose, with bicellular microhairs, short macrohairs and isolated silica bodies at the distal portion and along the margins; palea smooth; lodicules 2, ca. 0.4 mm long, hyaline, conduplicate; stamens 3, anthers 2 mm long, ferruginous; styles 2, free, stigma plumose, lateral. Caryopsis not seen.

Common name. "Grama-das-pedras" (Brazil).

Chromosome number. n = 10 (Davidse & Pohl, 1978; Pohl, 1980); 2*n* = 40, 60 (Gould & Soderstrom, 1967).

Distribution and habitat. This species grows from southern Mexico, Mesoamerica, Colombia, Venezuela, Guyana, and Surinam to Bolivia, Paraguay, and central and southern Brazil, mainly in savannas on sandy soils with rocky outcrops. It is frequent in areas with periodical fires, occasional in margins of streams, between 180 and 1800 m elevation.

Paspalum pectinatum is a member of section *Pectinata* by its winged and cordate upper glume. This species is related to *P. cordatum,* a species distinguished by its robust plants, 100–130 cm tall,

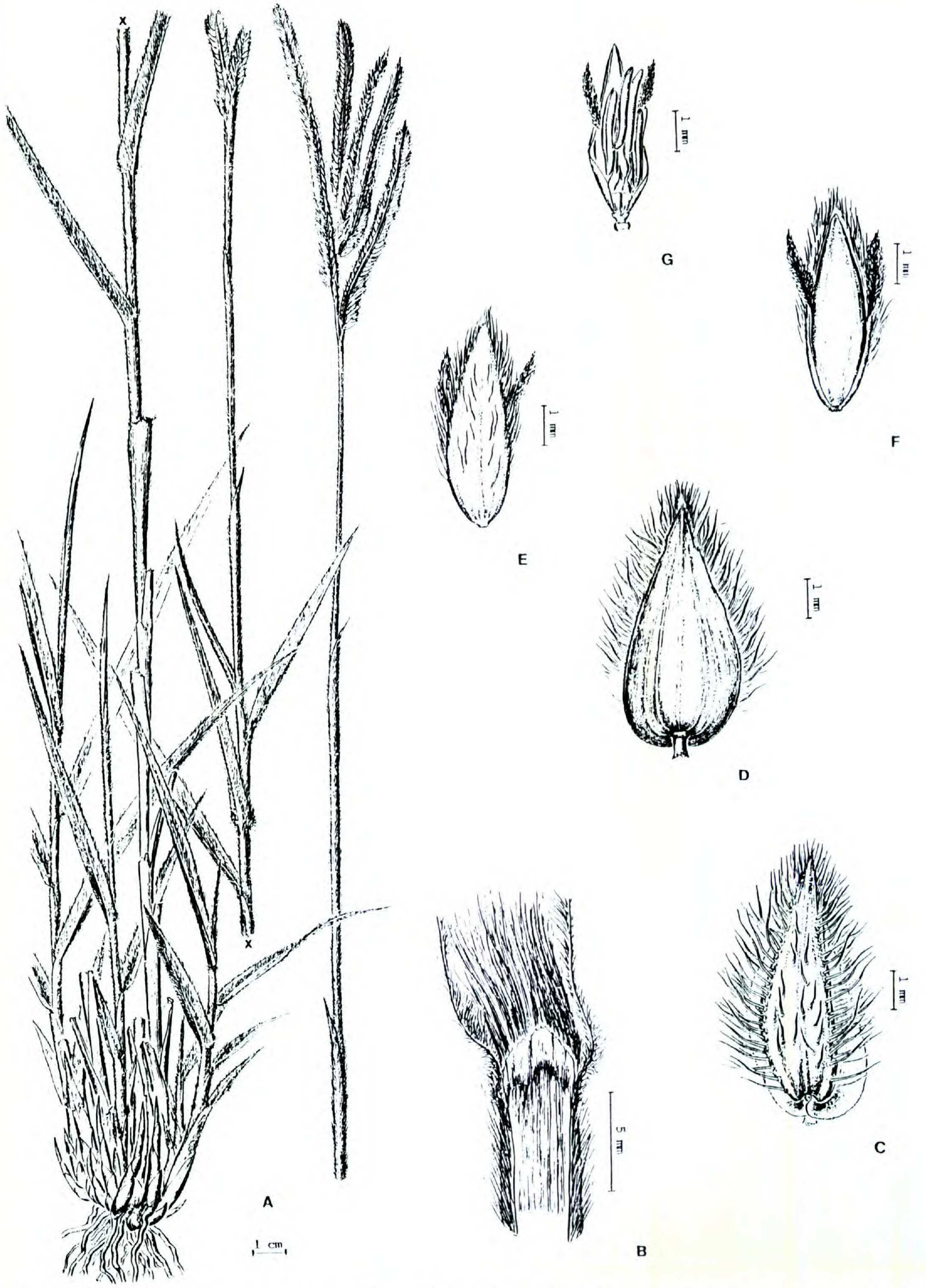

Figure 18. *Paspalum pectinatum.*—A. Habit. —B. Detail of ligule. —C. Spikelet, ventral view. —D. Spikelet, dorsal view. —E. Upper anthecium, dorsal view with lateral stigmatic plumules. —F. Upper anthecium, ventral view with lateral stigmatic plumules. —G. Upper palea, lodicules, anthers, and gynoecium. (Based on *Filgueiras 2459*, SI.)

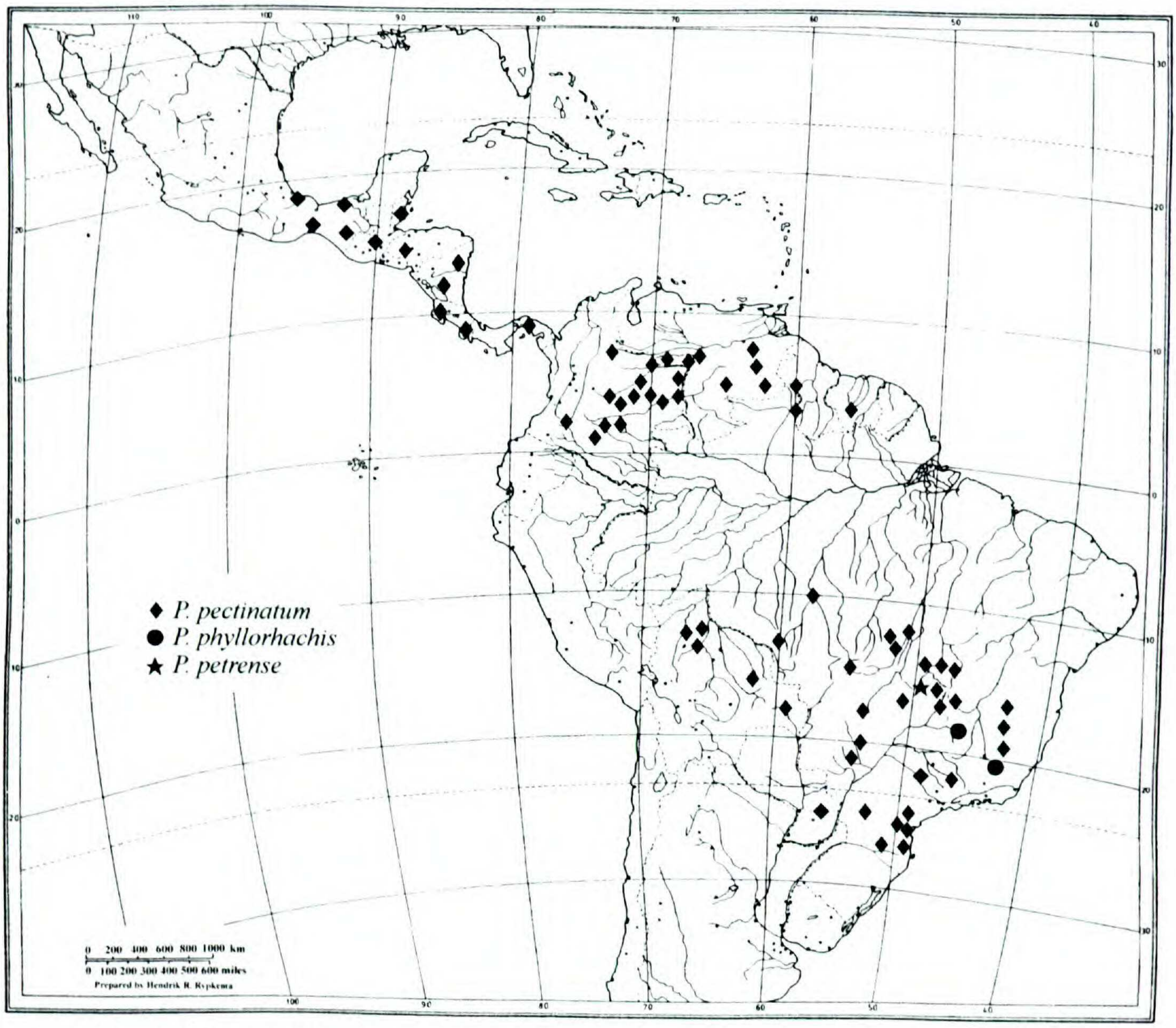
♦ P. pectinatum
● P. phyllorhachis
★ P. petrense
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 19. Distribution of *Paspalum pectinatum*, *P. petrense*, and *P. phyllorhachis*.

with 5 to 10 racemes per inflorescence, each raceme 12–16 cm long.

The basal portion of the plant is usually covered with remains of burnt sheaths, which probably act as a protection for the renewal buds.

The specimens *Fonseca et al. 153*, *Oliveira et al. 763*, and *Filgueiras 2459*, collected in Goiás, Niquelândia, Brazil, have 8 to 9 internodes with leaf blades arranged along the floriferous culms.

There is a papyraceous bract at the base of the inflorescence, as in *Rivera 3*, *Pinto & Sastre 1066*, *Rivera L-141*, *Davidse 5321*, and *Cuatrecasas 7649-A*.

Representative specimens. BELIZE. **Belize:** along Manatee (or Coastal) Hwy., 7.4 km S of Turnoff to Gales Point, *Nee & Atha 46904* (MO). BOLIVIA. **Beni:** Prov. Vaca Diez: Riberalta, 65 km hacia Santa Rosa, cerca del desvío a Cobija, *Beck 20552* (K). **La Paz:** Prov. Iturralde, Luisita, *Haase 630* (K, MO). **Santa Cruz:** Chiquitos, 4 km W of Santiago de Chiquitos, *Killeen 2782a* (MO, US). BRAZIL. **Distrito Federal:** Brasília, lago Sul, *Zuloaga 3839* (SI). **Goiás:** Mun. Niquelândia, Macedo, ca. 20 km de Niquelândia, *Filgueiras 2455* (MO); Campo de Pichoce, *Glaziou 22427* (BM, K, MO, P, US). **Mato Grosso:** Expedition Base Camp, *Argent 6766* (K, P, US); ca. 70 km N of Xavantina, *Irwin & Soderstrom 6758* (K, MO, SI). **Minas Gerais:** Serra do Espinhaço, ca. 10 km SW of Diamantina, *Anderson et al. 35213* (MO); Diamantina, Serra de San Antonio, *Chase 10350* (MO, US). **Paraná:** Ponta Grossa, *Araujo 104* (SI); Jaguariaiva, *Dusén 16057* (MO, P, SI). **Santa Catarina:** Campo Novo, Mafra, *Klein 3916* (US). **São Paulo:** Bôa Vista, 4–5 km SE da Estação Eng. Hermilo, *Machado de Campos 111* (US). **Without locality:** *Sellow 1232*, *1239* (B). COLOMBIA. **Arauca:** N del río Tame, *Blydenstein 734* (COL). **Boyacá:** near Orocué, *Haught 2709* (COL). **Caquetá:** Mun. San Vicente del Caguán, Hato Caquetania, *Bentacur & Porras 1510* (MO). **Cauca:** Chisquito, *Asplund 10633* (US); Río Guaviare, San José del Guaviare, *Cuatrecasas 7649-A* (COL, US). **Cundinamarca:** savanna of San Martín, SE of Bogotá, *Shaw s.n.* (US). **Guaviare:** Mun. San José del Guaviare, Inspección de La Fuga, *Giraldo-Canas & López 2631* (MO). **Meta:** 20 km SE of Villavicencio, *Alston 7569* (BM, COL, US); Mun. Puerto Gaitán entre Carimagua y El Porvenir, *Rivera 3* (COL). **Santander:** La Laguna, carretera Lebrija–Pantano, *Rivera L-141* (COL). **Vichada:** Parque Nacional Natural Tuparro, *Barbosa & Zarucchi*

3032 (MO); ca. 45 km E of Cumaribo along dirt road between Las Gaviotas and Santa Rita, *Davidse & Llanos 5321* (COL). COSTA RICA. **Guanacaste:** Comelco, W of Bagaces, *Heithanus 163* (MO). **San José:** Cantón de Acosta, Fila Bustamante, *Morales 4395* (MEXU, MO). **Puntarenas:** Buenos Aires, *Pohl & Clark 13922* (MO). GUATEMALA. N of the San Pedro, *Semple 150* (US). GUYANA. Hillsides, Amai, *Graham 520* (K). HONDURAS. **Copán:** Hacienda Espíritu Santo, *Blake 7445* (US). MEXICO: **Chiapas:** Mun. Palenque, 2–4 km N of La Victoria and 7–9 km NWN of Palenque, *Davdise 20544* (MEXU, MO). **Oaxaca,** Mun. Sta. María Chimalapa, El Ocotal Grande, ca. 5 km al E de Sta. María, *Hernández 2283* (MO). **Tabasco:** km 64 rumbo Huimanguillo-Fco. Rueda al O de Huimanguillo, *Hill & Cowa 1548* (MEXU). **Veracruz:** a 11 km del entroque Las Choapas con la carretera Cardenas–Coatzacoalcos, *Orozco 182* (MEXU). NICARAGUA. **Chontales:** 15 km SE of Juigalpa, along Hwy. 7, *Pohl & Davidse 12361* (MO). **Zelaya:** near Cano Alamikamba, 26.5 km SE of El Empalme by road to Limbaika, *Kral 69245* (MO). PANAMA. **Chiriquí:** Cerro Vaca, eastern Chiriquí, *Pittier 4351* (US); Cerro Campana, *Lazor 3350* (MO). SURINAM. Sipaliwini savanna, *Rombouts 308* (US). PARAGUAY. **Canendiyú:** Mbaracayú Natural Reserve administered by Fundación Moisés Bertoni, 24°11′S, 55°16′W, *Zardini & Ramirez Benítez 51117* (MO). VENEZUELA. **Amazonas:** E of Caño Parucito and N of its tributary Caño Majagua, *Jangoux 10153* (MO). **Apure:** Distrito Pedro Camejo, 22 km W de Galeras de Cinaruco, *Davidse & González 15652* (MO). **Bolívar:** SW of La Vergareña, S of Ciudad Bolívar, *Alba 53–23* (US).

20. Paspalum petrense A. G. Burman, Kew Bull. 35: 297. 1980. TYPE: Brazil. Goiás: Serra de Pirineus, ca. 20 km E of Pirenópolis, 8 Apr. 1979, *T. S. Filgueiras & A. G. Burman 430* (holotype, K!; isotypes, IBGE!, SP not seen, RB-217458!). Figures 19, 20.

Caespitose perennial; culms erect, 70–90 cm tall, unbranched; internodes terete, hollow, glabrous or sparsely pilose toward the summit; nodes glabrous. Sheaths 7–10 cm long, papillose-pilose toward the apex, overlapping, keeled. Ligules ca. 1 mm long, membranous, truncate; pseudoligule absent. Blades linear to linear-lanceolate, 10–19 cm long, 3–6 mm wide, pubescent, the margins scabrous, attenuate at the base, the apex acute. Peduncles 17–30 cm long, pilose at the apical portion. Terminal inflorescences 8–15 cm long, 4–7 cm wide; main axis glabrous; pulvini pilose; racemes 3 to 5, 3–6 cm long, alternate, ending in a naked point; rachis of the racemes (6.5–)7–7.5 mm wide, foliaceous, glabrous, green to purple, with anastomosed veins on the wings, the margins slightly scabrous; pedicels 0.4–0.6 mm long, hispid, laterally inserted in the spikelets; spikelets paired, the basal one sometimes reduced or aborted, arranged in 2 to 4 series. Spikelets ellipsoid, 3–3.5 mm long, 1–1.1 mm wide, long-acuminate, pilose, pale, upper glume and lower lemma subequal, with an annular thickening at the base. Upper glume membranous to hyaline, 3-nerved, hairy on the lower half, the margins papillose-pilose. Lower lemma membranous to hyaline, acuminate, 3-nerved, pilose on the lower half with hairs shorter than those of the upper glume. Upper anthecium ellipsoid, 2.8–3 mm long, 0.6–0.8 mm wide, membranous, shiny, with a tuft of hairs at the apex, otherwise glabrous; upper lemma and upper palea with bicellular microhairs and papillae all over the surface and silica bodies at the apex; lodicules 2, 0.1 mm long; stamens 3; stigma plumose. Caryopsis not seen.

Distribution and habitat. Endemic to central Brazil, Goiás, where it is present in rocky soils on mountain slopes, at an elevation of 1200 m.

Paspalum petrense is related to *P. heterotrichon* (see observations under this species) and *P. trachycoleon*. *Paspalum petrense* differs from *P. trachycoleon* by its unbranched culms (vs. branching culms), rachis (6.5–7.5 mm vs. 4–6 mm wide), the upper glume long-acuminate (vs. acute to acuminate), and lower lemma long-acuminate, pilose, not sulcate, and with inconspicuous nerves (vs. acute, glabrous or with short, apical hairs, sulcate, and with conspicuous nerves).

21. Paspalum phyllorhachis Hackel, Oesterr. Bot. Z. 51: 240. 1901. TYPE: Brazil. Minas Gerais: without locality, 1872, *A. F. M. Glaziou 20078* (holotype, W!; isotypes, B!, K! photo, SI!, US-2855768! photo, SI!). Figures 19, 21.

Shortly rhizomatous perennial; culms 70–170 cm tall, 2–7 mm diam., erect or climbing, bambusiform, branching at the lower and middle nodes; internodes 5–8 cm long, glabrous, terete, hollow, lignified; nodes glabrous, brown. Sheaths 5–8 cm long, glabrous or pilose at the upper portion, keeled, the margins smooth, glabrous. Ligules membranous, 1.5–2 mm long, truncate to rounded at the apex, decurrent; pseudoligule absent. Leaf blades linear-lanceolate, 7–17 cm long, 0.4–1.3 cm wide, rounded, long-acuminate at the apex, with the abaxial surface glabrous to pilose and the adaxial surface densely pilose, margins smooth to scabrous. Peduncles exserted, glabrous or pilose toward the distal portion. Terminal inflorescences exserted, 10–13 cm long, 1.5–3 cm wide; main axis 4–9.5 cm long, 0.5 mm diam., glabrous or pilose; racemes 7 to 14, (2.5–)3.5–5 cm long, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 4–6 mm wide, foliaceous, with anastomosed nerves on the wings, glabrous, brown; pedicels 0.8 mm long, hispid, laterally inserted in the spikelets; spikelets paired, imbricate in 4 series. Spikelets

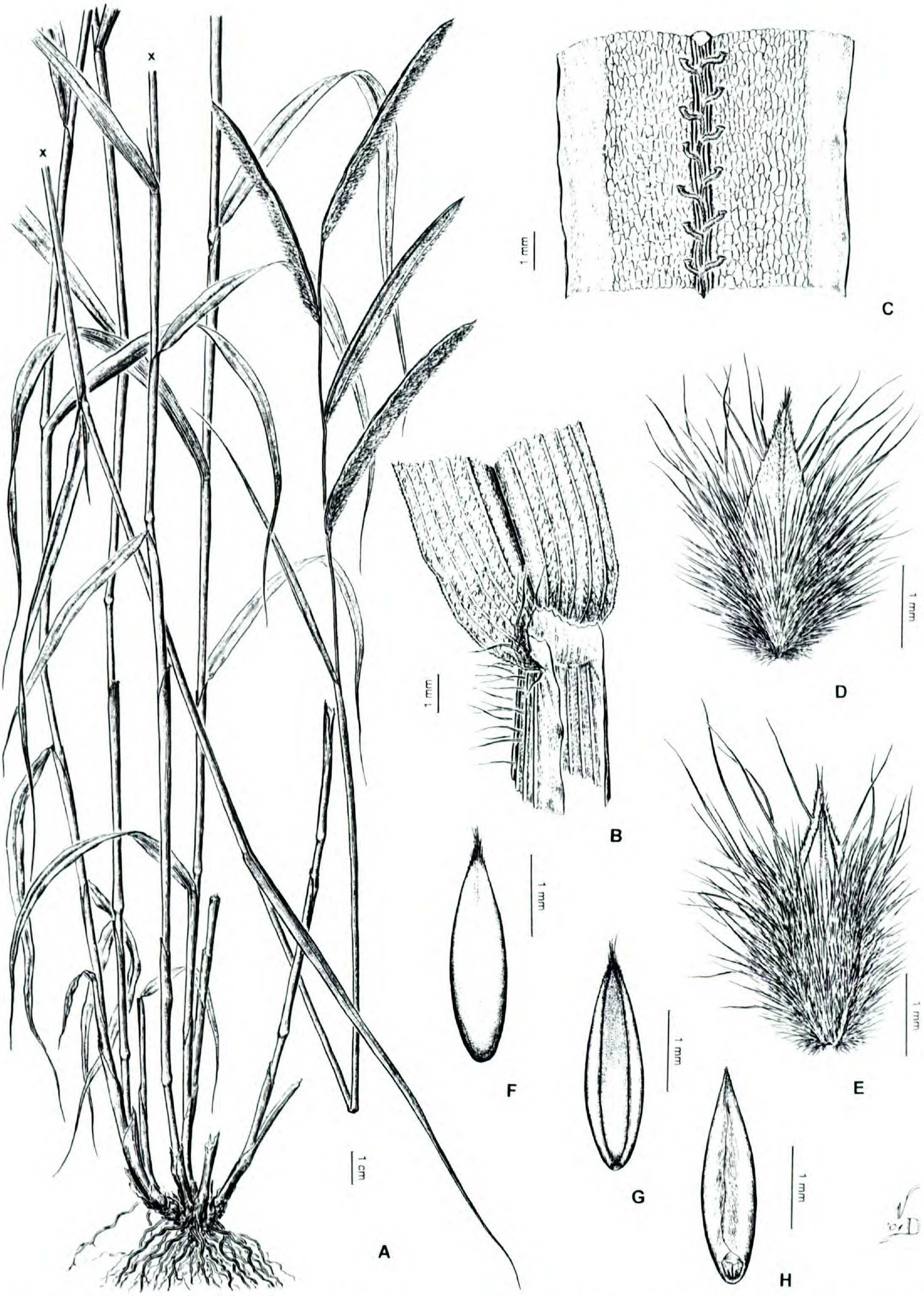

Figure 20. *Paspalum petrense.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea and lodicules. (Based on *Filgueiras & Burman 430.*)

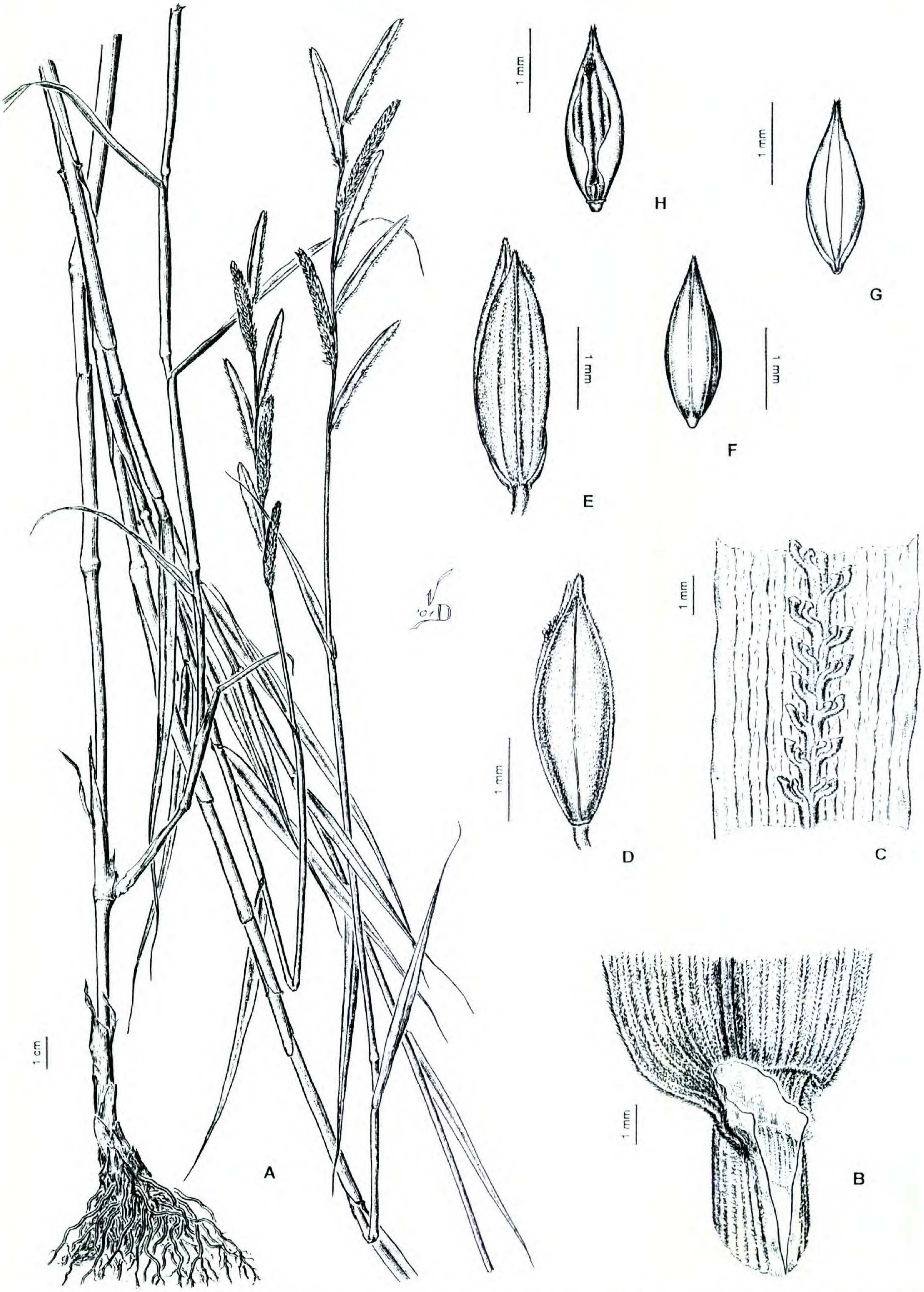

Figure 21. *Paspalum phyllorhachis*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and anthers. (A based on *Chase 8975*, US; B–H based on *Glaziou 20070*, P.)

ellipsoid, 2.3–2.8 mm, 0.8–1 mm wide, glabrous, upper glume and lower lemma subequal, scabrous at the upper margins. Upper glume as long as the spikelet, acuminate, hyaline to membranous, 3-nerved. Lower lemma glumiform, acuminate, membranous, 3-nerved. Upper anthecium lanceolate, 2.1–2.7 mm long, 0.7–1 mm wide, membranous, scabrous at the apex, otherwise glabrous; upper lemma and palea with conspicuous, simple papillae and bicellular microhairs all over the surface, and prickles at the apical portion; stamens 3, anthers 1.5 mm long; stigma plumose. Caryopsis not seen.

Distribution and habitat. Endemic to Brazil, Minas Gerais, where it is found in open fields between 1200 and 1400 m elevation.

Paspalum phyllorhachis is related to *P. petrense* and *P. trachycoleon* by its paired spikelets. It differs from both species by these spikelets being glabrous.

Glabrous and pilose spikelets were occasionally observed in the specimen *Magalhães Gomes 908*, with sparse hairs toward the apical margins of the upper glume.

Representative specimens. BRAZIL. **Minas Gerais:** Serra do Curral, S of Belo Horizonte, *Chase 9325* (US), *8975* (US); Rios das Pedras a Matto Grande, *Glaziou 20070, 20076* (P); Belo Horizonte, *Magalhães Gomes 908* (US-1762607).

22. Paspalum polyphyllum Nees ex Trinius, Gram. Panic. 114. 1826. *Paspalum polyphyllum* Nees, Fl. Bras. Enum. Pl. 2: 41. 1829, hom. illeg. TYPE: Brazil. Chapada, "in campis siccis pr. Mariannam," 1824, *G. H. von Langsdorff s.n.* (holotype, LE!; isotypes, K! photo, SI!, US-2855764! photo, SI!). Figures 7, 22.

Paspalum blepharophorum Roem. & Schult. var. *tenue* Döll, in Mart., Fl. Bras. 2(2): 67. 1877. TYPE: Brazil. Without locality, *L. Riedel s.n.* (lectotype, designated here, W!; isolectotype, G!).

Paspalum macroblepharum Hack., Oesterr. Bot. Z. 51: 196. 1901. TYPE: Brazil. Rio de Janeiro: without locality, 1887, *J. Arechavaleta 41* (holotype, W!; isotype, US-2855810! photo, SI!).

Paspalum bicilium Mez, Repert. Spec. Nov. Regni Veg. 15: 27. 1917. TYPE: Brazil. Goiás: Fazenda do Siriaco, cascada do Rio Macaco, 12 July 1895, *A. F. M. Glaziou 22563* (lectotype, designated here, B!; isolectotypes, BR not seen, K!, P! photo, SI!, US-2942158!).

Caespitose perennial, with long, arcuate rhizomes, cataphylls coriaceous, villous; culms (10–)25–90 cm tall, 0.1–0.2 cm diam., rigid, branched or unbranched, erect, occasionally decumbent; internodes 1–10 cm long, terete, hollow, glabrous; nodes brown, glabrous or shortly pilose. Sheaths 1.5–8 cm long, usually longer than the internodes, glabrous to hirsute, with tuberculate hairs, the margins glabrous or shortly ciliate. Ligules 0.4–2.5 mm long, membranous, brown, glabrous; pseudoligule, when present, a tuft of rigid hairs 2.4–5 mm long; collar glabrous to shortly pilose. Leaf blades linear to linear-lanceolate, 4–13 cm long, 0.1–0.6 cm wide, flat, rigid, ascendent, glabrous to papillose-pilose on both surfaces, narrow or rounded at the base, the apex subulate, the margins short to long papillose-pilose. Peduncles exserted, up to 30 cm long, terete to filiform, glabrous to hirsute in the distal portion. Terminal and axillary inflorescences exserted; terminal inflorescences 4–12 cm long, 0.4–3(–4) cm wide; main axis absent or 1–4(–7) cm long, sulcate, glabrous to hirsute; pulvini shortly pilose, with white hairs up to 0.6 mm long; axillary inflorescences 4–7 cm long, 0.5–3 cm wide; racemes 1 to 4(8), ascendent, slightly divergent from the axis, straight, alternate, ending in a naked point, sometimes in a spikelet; rachis of the racemes 3–10 cm long, 1–1.2 mm wide, pilose or with adaxial surface glabrous, green or tinged with purple, with anastomosed veins, the margins scabrous and covered with long hairs; pedicels unequal, up to 1.7 mm long, triquetrous, hispid; spikelets paired, densely arranged in 4 series, sometimes lower spikelet aborted. Spikelets long-ellipsoid, 1.4–3.8 mm long, 0.6–1.2 mm wide, acute, pilose, the margins rigid, purple, covered with long, ciliate spreading hairs; upper glume and lower lemma as long as the spikelet, hyaline. Upper glume with corky margins covered with radiate, white hairs 2–7 mm long, alternating with shorter hairs 0.8–2 mm long, otherwise shortly pilose, 3-nerved. Lower lemma hyaline, the margins shortly pilose, hairs up to 0.5 mm long, the rest of the surface glabrous to sparsely pilose, convex and depressed toward the base, 3-nerved. Upper anthecium long-ellipsoid, 1.2–3.6 mm long, 0.6–0.8 mm wide, acute, membranous, pale, with bicellular microhairs and simple papillae all over the surface and macrohairs and silica bodies toward the apex of the upper lemma and palea, upper lemma 3-nerved; lodicules 2, ca. 0.2 mm long, conduplicate, hyaline; stamens 3, anthers 0.8–2 mm long. Caryopsis long-obovoid, 0.8–1.3 mm long, 0.4–0.6 mm wide; hilum linear, ⅓ the length of the caryopsis; embryo ⅓ to ½ the length of the caryopsis.

Common name. "Capim-lanoso" (Brazil).

Distribution and habitat. From Venezuela and Colombia to central and southern Brazil, Bolivia, Paraguay, northeastern Argentina, and Uruguay. This species grows in open fields and savannas, on

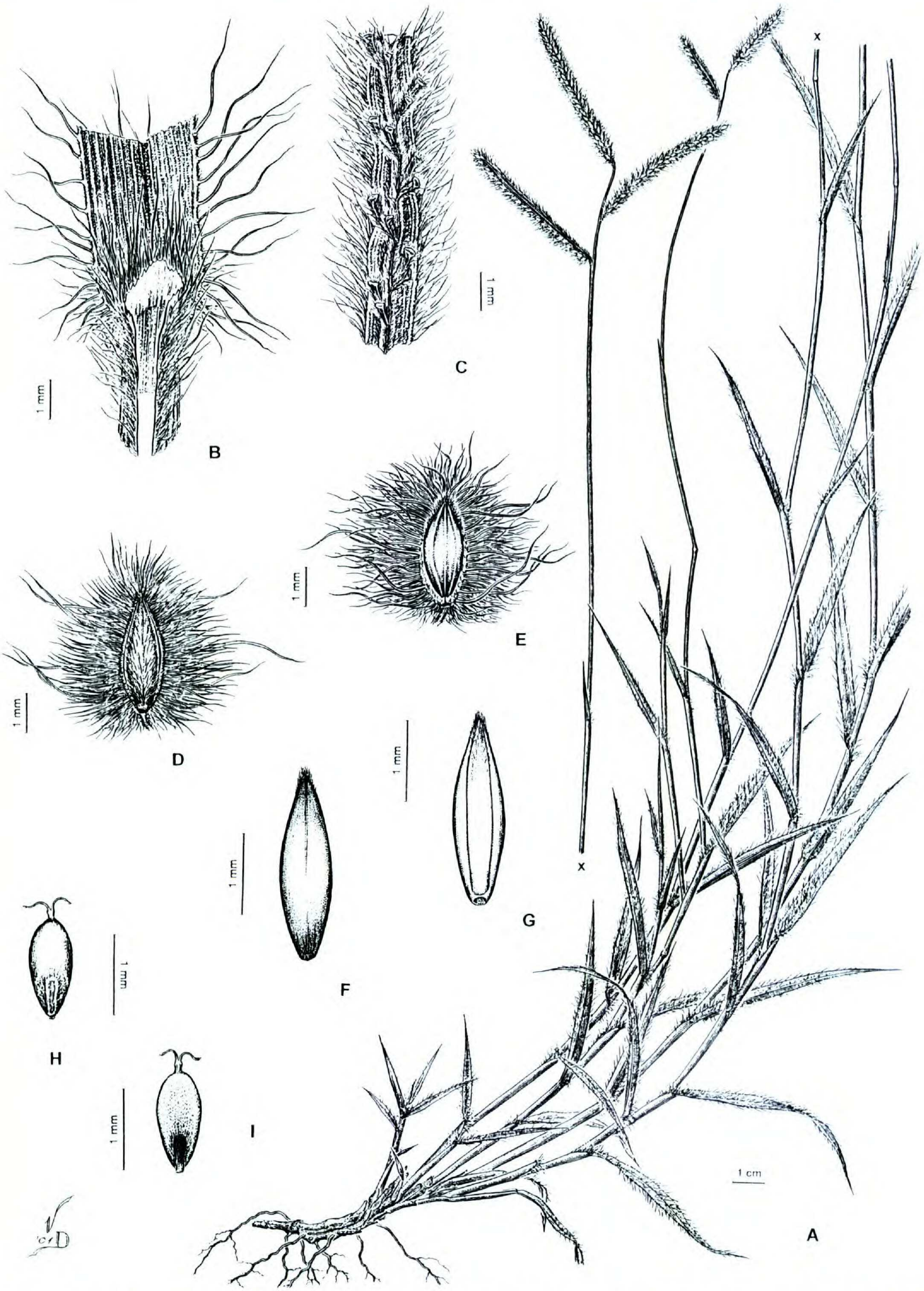

Figure 22. *Paspalum polyphyllum*.—A. Habit. —B. Detail of ligule. —C. Portion of rachis. —D. Spikelet, dorsal view. —E. Lemma, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (Based on *Smith & Klein 12106*, US.)

rocky, sandy soils, occasionally in swamps, between 0 and 2500 m.

Paspalum polyphyllum shows a high degree of plasticity in its vegetative characters, such as plant height, branching, blade pilosity, and size of inflorescences and spikelets. This species has two different growing patterns; one of them, with simple culms bearing larger inflorescences and spikelets of different size, from 2.6 to 3.6 mm long (e.g., *Swallen 8772, Smith & Klein 12106, Hassler 11561, Schulz 17275, Archer & Barreto 4995*, and *Fiebrig 6222*) or more than 4 mm, e.g., *Rojas 13933*, which also have inflorescences more than 19 cm long, racemes 11–13 cm long, and spikelets 4–4.2 mm long. The other phase is characterized by its culms profusely branching at the middle nodes, with smaller inflorescences and spikelets ca. 2 mm long (as in *Irwin et al. 16232a, 17256, Killeen 2795, Hunt & Ferreira Ramos 6012, Hunt 6246*, and *Chase 9148*). Also, both phases can be found in a single collection, e.g., *Swallen 9150*, where simple, erect culms up to 40 cm tall, with spikelets 3 mm long, are mixed with more delicate culms in which spikelets are 2 mm long. It is noteworthy to mention that the type material of *P. polyphyllum* belongs to the second phase of development.

When studying type material of *Paspalum bicilium* and *P. macroblepharum* it became evident that they belong to the branching phase of *P. polyphyllum*, with spikelets up to 2 mm long.

Doell (1877) cited, following the concept of Trinius (1828–1836, figs. 134, 144), under *P. blepharophorum* and *P. distichophyllum* what here is considered *P. polyphyllum*, including in *P. blepharophorum* specimens of the unbranching phase and in *P. distichophyllum* specimens of the branching one. Both species are here considered synonyms of *P. humboldtianum* (see synonymy under this species).

Doell (1877) cited three syntypes when describing *P. blepharophorum* var. *tenue*, of which *Riedel s.n.* was here selected as lectotype of the species; of the remaining syntypes, *Sellow s.n.* also belongs to *P. polyphyllum*, and *D'Orbigny 168*, from Chuquisaca, Bolivia, probably belongs to *P. humboldtianum.*

The number of racemes is higher, ranging from 4 to 12, in the specimen *Chase 9369*.

Mez (1917) cited two syntypes when describing *P. bicilium, Glaziou 22562* and *22563*, of which the latter has been selected as lectotype of the species.

According to Rosengurtt et al. (1970) this species is a low-yield forage grass.

Representative specimens. ARGENTINA. **Chaco:** Dpto. San Fernando, Fontana, *Meyer 2090* (LIL); Dpto. 1° de Mayo, Colonia Benítez, *Schulz 17275* (G, MO, SI). **Corrientes:** Dpto. Paso de Los Libres, Campo Militar Gral. Avalos, *Carnevali 3200* (CTES, LIL). **Misiones:** Dpto. San Ignacio, sobre Ruta Prov. 210 m, a 7 km Ayo. Horqueta, *Honfi 98* (LIL, MO); Puerto Nuevo, *Schwarz 2214* (B, LIL, US). BOLIVIA. **La Paz:** Puente Villa-Yungas, *Cárdenas 3606* (US). **Santa Cruz:** Prov. Chiquitos, S slope of the Serrania de Santiago, *Daly et al. 2171* (MO, SI); Chiquitos, Serrania de Santiago, *Killeen 2795* (MO); Buena Vista, *Steinbach 6808* (BM, G, K, MO, W, US). BRAZIL. **Bahia:** Mun. Palmeiras, Pai Inácio, BR-242, km 232, *Mori 13303* (K, MO); Dpto. Palmeiras, Morro do Pai Inacio, *Zuloaga & Morrone 6944* (IBGE, SI). **Distrito Federal:** a 32 km do CENARGEM, *Borges Dias Vieira 189* (MO); Parque Municipal do Gama, ca. 20 km S of Brasília, *Irwin & Soderstrom 5800* (MO, SI, US). **Goiás:** Serra do Caiapó, ca. 33 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7069* (K, MO, SI); between Jataí and Caiaponia, 45 km from Caiaponia, *Hunt 6246* (K, US); Serra Azul, about 7 km W of the Barra do Garcas, *Hunt & Ramos 6012* (K, US). **Mato Grosso:** ca. 6 km S of Xavantina, *Argent et al. 6460* (P, US); Serra do Roncador, Rio Turvo, *Irwin et al. 16232a* (MO); summit, Serra Azul, *Irwin et al. 17256* (US). **Minas Gerais:** without locality, *Glaziou 20082* (P, US, W); Serra do Cipó, Chapeu de Sol, Santa Luzia, *Archer & Barreto 4995* (US); Serra do Cipó, 110 km NE of Belo Horizonte, *Chase 9148* (MO); Ouro Preto, Villa Rica, *Chase 9369* (MO, US). **Paraná:** 13 km NE of Atuba (which is just outside of Curitiba) along Hwy. 116, *Davidse et al. 10967* (MO); Ponta Grossa, Fazenda de Criaçao, *Swallen 8772* (US). **Rio de Janeiro:** Itatiaia, *Brade & Vianna 20377* (US); environs de Rio de Janeiro, *Glaziou 17940* (G, MO, W). **Rio Grande do Sul:** Montenegro, *Araujo 144* (US); Pelotas, *Swallen 9150* (US). **Santa Catarina:** Mun. Mafra, campo 10 km NW of Mafra on the road to Barracas (20 km), *Smith & Klein 12106* (US). **São Paulo:** Est. Biológica do Inst. Bot. Paranpiacaba, *Dedecca 302* (US). COLOMBIA. **Boyacá:** Villa de Leyva cerca de Sáchica, *Saravia 4186* (COL). **Santander:** Mesa Los Santos, *Robinson & Beltran 3189* (US). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 6222* (BAA, BM, G, LIL, SI, US). **Amambay:** in campis arenosis Estrella, *Hassler 10209* (G, US). **Caaguazú:** Caaguazú, *Balansa 90a* (G, P). **Central:** in regione lacus Ypacaray, *Hassler 11501* (MO). **Cordillera:** Piribebuy, Colonia Pedro Caballero, *Rojas 13404* (LIL-561328). **Guairá:** Borja, *Montes s.n.* (LIL-561328). **Paraguarí:** Cerro Peron, prés de Paraguarí, *Balansa 90* (BM, G, P, US, W). URUGUAY. **Artigas:** Artigas, *Berro 2680* (BAA, W). **Cerro Largo:** Palleros, *Herter 1755* (G, MO, US). **Flores:** Río Yí y Ayo, Matanzas, *Montoro s.n.* (US-1723957). **Paysandú:** Río Uruguay y Chapicuy, *Rosengurtt B-3197* (LIL, US). **Rivera:** Tranqueras, *Castellanos 17922* (LIL). **Tacuarembó:** without locality, *Osten 6632* (SI, US). VENEZUELA. **Lara:** Distr. Morán, Carretera de Humocaro Bajo via Buenos Aires, *van der Werff & Rivero 7863* (MO). **Trujillo:** La Cristalina, *Tamayo 1867* (US).

23. Paspalum reticulinerve Renvoize, Kew Bull. 50: 339, fig. 1 A–G. 1995. TYPE: Bolivia. La Paz: Prov. Iturralde, Siete Cielos, Río Manupare, ca. 2.5 km al E, 12°27'S, 67°37'W, 180 m, 8 June 1987, *J. C. Solomon 17003* (holotype, LPB not seen; isotypes, K!, MO!). Figure 14.

Shortly rhizomatous perennial; floriferous culms (70–)90–120(–140) cm tall, 0.3 cm diam., erect, branched or unbranched; internodes finely striate, glabrous, hollow; nodes 5 to 7, compressed, brown, glabrous. Sheaths 15–24 cm long, usually longer than the internodes, keeled toward the upper portion, glabrous to hirsute, the inner surface red-tinged-brown, shiny, the margins membranous, glabrous. Ligules membranous, 1–2.5 mm long, brown, glabrous; pseudoligule absent or a tuft of hairs 5–7 mm long. Blades linear-lanceolate, 17–40 cm long, 0.3–0.8 cm wide, flat, glabrous to hirsute, the base attenuate and the apex acute, the margins involute, with long hairs toward the lower portion, otherwise scaberulous. Peduncles up to 40 cm long, terete, glabrous. Terminal inflorescences exserted, 5–15 cm long; main axis absent or up to 1 cm long, flat, glabrous; pulvini shortly pilose; racemes (1)2(3), 5–15 cm long, ending in a naked point; rachis of the racemes winged, 1–1.8 mm wide, green or tinged with purple, glabrous to sparsely pilose, the midnerve scabrous and margins scaberulous to papillose-pilose; pedicels unequal, flat, scaberulous; spikelets paired, densely imbricate in 4 series. Spikelets broadly ovoid, 4.8–6 mm long, 3–4 mm wide, dorsiventrally compressed, plano-convex, winged, cordate, ciliate on the margins of the upper glume. Upper glume as long as the spikelet, 7(–9)-nerved, winged, with just 3 central nerves reaching the apex, membranous, ciliate, cordate, the apex acute. Lower lemma 3.5–4.4 mm long, 2 mm wide, 3-nerved, glabrous, coriaceous, corrugated and rounded at the base, the margins winged, shortly ciliate. Upper anthecium ellipsoid, 2.8–3.6 mm long, 0.8–1.5 mm wide, plano-convex, papyraceous, pale; upper lemma with simple papillae, bicellular microhairs, and macrohairs toward the apical portion; upper palea with papillae and bicellular microhairs; lodicules 2, ca. 0.4 mm long, hyaline, conduplicate; stamens 3, anthers 1.6 mm long; styles 2, stigma plumose, lateral. Caryopsis obovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic, embryo ½ the length of the caryopsis.

Iconography. Renvoize, Gramíneas de Bolivia: 450, fig. 97. 1998.

Distribution and habitat. Present in Bolivia, in La Paz and Santa Cruz, and Brazil, in the states of Pará, Tocantins, and Mato Grosso. It grows in open fields and "campos rupestres," between 100 and 900 m.

Paspalum reticulinerve is a member of section *Pectinata*, where it is related to *P. aspidiotes* and *P. imbricatum*; the latter has glabrous, solitary spikelets and inflorescences with (2)5 to 7(11) racemes. When describing *P. reticulinerve*, Renvoize (1995) related this species to *P. aspidiotes*, from which this author distinguished *P. reticulinerve* by the densely pubescent, attenuate leaf blades, a ciliate rachis, and smaller spikelets. Later, Renvoize (1998) segregated *P. aspidiotes* from *P. reticulinerve* by having glabrous and cordiform leaf blades, the rachis scabrous, and a smooth upper anthecium. The study of type material of both species, and specimens from Bolivia and Brazil, allowed us to conclude that the real identity of *P. aspidiotes* had been misunderstood: this taxon is clearly separated from *P. reticulinerve* by having solitary spikelets 6.5–7.5 mm long. Also we concluded that the pilosities of leaf blades and inflorescences are unreliable characters to segregate both species: in the specimen *Kuhlmann 1671* the rachis of the racemes is sparsely pilose, with hairs up to 0.4 mm long, while in *Killeen 6541* pilose and attenuated leaf blades are present together with a glabrous rachis of the racemes. A similar situation is present in the specimen *Plowman et al. 8949*, with the rachis of the racemes sparsely pilose.

Representative specimens. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parque Nacional Noel Kempff M., Serranías de Caparuch, *Killeen 6541* (MO); Parque Nacional Noel Kempff M., *Killeen et al. 4824* (SI). BRAZIL. **Mato Grosso:** Serra do Tombador, estrada do Diamantina, *Kuhlmann 1671* (US). **Pará:** Marabá, Serra dos Carajás, *Cavalcante 2131* (US); Mun. Conceição do Araguaia, about 4 km W of town center along hwy. PA-150, *Plowman et al. 8949* (MO, US). **Tocantins:** Mun. Couto Magalhães, Pequizeiro along GO-70, *Plowman et al. 9133* (MO, US).

24. Paspalum stellatum Humboldt & Bonpland ex Flüggé, Gram. Monogr., Paspalum 62. 1810, as "Paspalus stellatus." TYPE: Colombia. Without locality, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, B-W not seen; isotypes, BM!, US-80051!). Figure 23.

Paspalum stellatum Humb. & Bonpl. ex Flüggé var. *monostachyum* Nees, Fl. Bras. Enum. Pl. 2: 78. 1829, as "Paspalus stellatus var. monostachyus." TYPE: Brazil. Without locality, *F. Sellow 1242* (holotype, M not seen; isotypes, B not seen, P!, US-80052! photo, SI!).

Paspalum stellatum Humb. & Bonpl. ex Flüggé var. *distachyum* Nees, Fl. Bras. Enum. Pl. 2: 78. 1829, as "Paspalus stellatus var. distachyus." TYPE: Brazil. "In apricis arenosis prope Tejuco," *G. H. von Langsdorff s.n.* (holotype, LE not seen).

Paspalum cujabense Trin., Sp. Gram. 3: pl. 284. 1829–1830. TYPE: Brazil. Mato Grosso: Cuiabá, in graminosis humidis, 1829, *G. H. von Langsdorff s.n.* (holotype, LE!; isotypes, K! photo, SI!, US-80050!).

Paspalum wagenerianum Schltdl., Linnaea 26: 13. 133. 1854. TYPE: Venezuela. Distrito Federal: Surfacecas, *Wagener 396* (type not seen).

Paspalum splendens Hack. var. *sphacelatum* Hack., Oesterr. Bot. Z. 51: 239. 1901. TYPE: Brazil. Goiás:

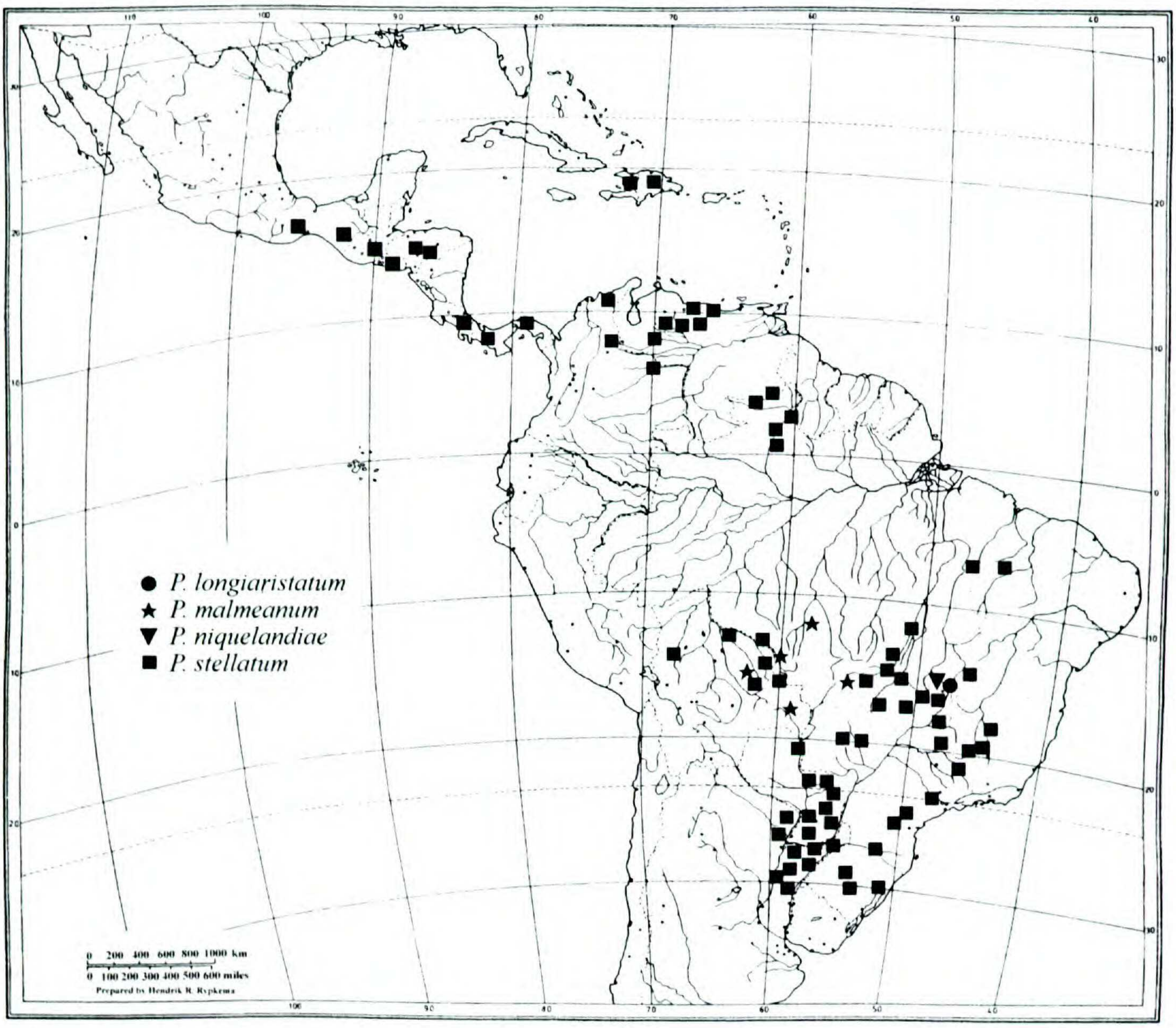
● P. longiaristatum
★ P. malmeanum
▼ P. niquelandiae
■ P. stellatum
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 23. Distribution of *Paspalum longiaristatum*, *P. malmeanum*, *P. niquelandiae*, and *P. stellatum*.

Santa Luzia, 8 Abr. 1895, *A. F. M. Glaziou 22550* (holotype, W!; isotypes, P!, US-2856000!, US-2856001! photo, SI!, US-555446!).

Paspalum stellatum Humb. & Bonpl. ex Flüggé f. *hirsuta* Hack., in Stuck., Anales Mus. Nac. Buenos Aires 21: 28. 1911. TYPE: Argentina. Chaco: Resistencia, 31 Mar. 1908, *H. Mercenaro s.n., leg. T. J. V. Stuckert 18694* (holotype W!; isotypes, CTES!, SI! p.p., US-80049! photo, SI!).

Caespitose, shortly rhizomatous perennial, cataphylls pilose; culms 25–100 cm tall, 0.1–0.2 cm diam., unbranched, erect to geniculate, fasciculate at the base; internodes 3–18 cm long, terete, hollow, glabrous; nodes 3–6, brown, glabrous to shortly pilose. Sheaths 4–8 cm long, striate, glabrous to hirsute, with tuberculate, deciduous hairs, the margins membranous; basal sheaths overlapping. Ligules membranous, short, 0.2 mm long, brown, glabrous; pseudoligule a tuft of short hairs intermixed with long hairs up to 0.5 mm long; collar glabrous. Leaf blades filiform, 8–27 cm long, 0.1–0.3 cm wide, mainly basal, ascendent, rigid, narrowed at the base, apex acuminate, the margins involute, the basal ones ciliate, both surfaces sparsely papillose-hirsute covered with long, tuberculate hairs, or the adaxial surface glabrous. Peduncles up to 25 cm long, glabrous to shortly hirsute. Terminal inflorescences exserted; main axis absent; pulvini shortly pilose, with (1–)2 papyraceous bracts, up to 4 mm long, at the base; racemes 1, rarely 2 conjugated, falcate, ending in a naked point; rachis of the racemes broadly winged, 2–15 cm long, (4–)5–10 mm wide, glabrous to shortly hispid on the adaxial surface, green to purple, midnerve prominent, the margins membranous to hyaline, nerveless, brown, flat to plicate and enclosing the spikelets; pedicels 0.1–0.2 mm long, shortly hirsute, with radiate hairs at the apex; spikelets solitary, arranged in 2 series. Spikelets ovoid to ellipsoid, 2.4–3.9 mm long, 1.2–1.6 mm wide, plano-convex, acute, pale or tinged with purple toward the apex or all over the surface, villous, the upper glume and lower lemma as long as the spikelet. Upper glume membranous, 2–3-

nerved, the central nerves inconspicuous or absent, with a tuft of hairs toward the base, glabrous on the rest of the surface, the margins papillose-pilose, with white hairs up to 4 mm long. Lower lemma glumiform, 2-nerved, the nerves marginal. Upper anthecium narrowly obovoid, 1.8–2.9 mm long, 0.8–1 mm wide, 0.4–1 mm shorter than the upper glume and lower lemma, membranous, pale, smooth, glabrous, shortly stipitate, easily deciduous at maturity; upper lemma 5-nerved, smooth, with sparse bicellular microhairs; lodicules 2, 0.2 mm long; stamens 3, anthers 1.8–2 mm long. Caryopsis obovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic; embryo ½ the length of the caryopsis or slightly shorter.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 16, fig. 1. 1929. Luces de Febres, Las Gramíneas del Distrito Federal: 115, fig. 65. 1963. Burkart, Fl. Il. Entre Ríos: 377, fig. 156. 1969. Rosengurtt et al., Gramíneas uruguayas: 348, fig. 151. 1970. Pohl, Fieldiana, Bot. n.s. 4: 454, fig. 171. 1980. Smith et al., Fl. Il. Catarinense: 922, fig. 185. 1982. Rodríguez, Ernstia 8(2–3): 46. 1998. Renvoize, Gramíneas de Bolivia: 452, fig. 98, D. 1998.

Common name. "Capim-estrela" (Brazil).

Chromosome number. $2n = 32, 52$ (Honfi et al., 1991[1990]); $2n = 20, 32$ (Killeen, 1990).

Distribution and habitat. From southern Mexico, Central America, and the Caribbean to South America, where it is found in Venezuela, Colombia, Bolivia, Brazil, Paraguay, and Argentina; cited for Uruguay by Rosengurtt et al. (1970). It grows in fields or savannas on sandy or rocky soils, or lateritic outcrops, between 0 and 2000 m elevation.

Paspalum stellatum is related to *Paspalum ceresia, P. eucomum,* and *P. malmeanum* by its winged and nerveless rachis of the racemes, with spikelets densely pilose. *Paspalum ceresia* differs by its glaucous plants, with filiform to linear-lanceolate leaf blades, 7–21 cm long, 0.3–1.5(–2) cm wide; inflorescences with two to seven racemes (rarely a solitary raceme), alternate, without a bract at the basal pulvini; and pedicels hispidulous and upper anthecium not stipitate. *Paspalum eucomum* is distinguished by having two conjugated racemes (rarely a third one) per inflorescence, rachis of the racemes 1.5–2.5(–4) mm wide, and upper anthecium as long as the upper glume and lower lemma. *Paspalum malmeanum* differs by its rachis of the racemes 1.2–2 mm wide, spikelets 1.6–2 mm long, and upper anthecium as long as the spikelet.

Compound papillae are occasionally present in the upper anthecium of specimens from Santa Cruz, Bolivia.

According to Rosengurtt et al. (1970) and Smith et al. (1982), this species is a low-yield forage grass.

Representative specimens. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 300* (LIL). **Corrientes:** Dpto. Goya, Paraje San Isidro, 46 km S de Goya, *Ahumada et al. 3541* (CTES, K, LIL). **Entre Ríos:** Dpto. Federación, Santa Ana, barrancas del Río Uruguay, *Burkart & Gamerro 21610* (SI). **Formosa:** Dpto. Laishí, without locality, *Joergensen 2882* (G, MO, SI, US). **Misiones:** Dpto. Capital, Posadas, La Granja, *Ekman 594* (US); Dpto. Candelaria, Santa Ana, *Montes 1953* (G, LIL, P, US, W). BOLIVIA. **Beni:** Prov. Iténez, Magdalena, *Moraes et al. 1713* (LPB, SI). **La Paz:** Chaquimayo–Apolo trail ca. 15 km NW of Apolo, *Gentry & Foster 71186* (MO). **Santa Cruz:** Prov. Velasco, San Ignacio, *Beck & Seidel 12330* (MO, SI); Ñuflo de Chávez, Concepción, *Killeen 2474* (MO, SI, US). BRAZIL. **Amazonas:** Uraricuera, *Myers 3404* (US). **Distrito Federal:** Brasília, campus da UNB, *de Jesus 16* (US). **Goiás:** Rio Cristal, 44 km by road SE of Cristalina, *Anderson 8286* (BM, MO, US); without locality, *Glaziou 22546* (G, K, P, W). **Maranhão:** Mun. Loreto, Ilha de Balsas region, *Eiten & Eiten 4417* (K, US). **Mato Grosso:** Mun. Terenos, Faz. Modelo (IPEAO), *Allem & Vieira 2236* (MO); ca. 270 km N of Xavantina, *Ratter et al. 1915* (K, US). **Minas Gerais:** Uberaba, *Chase 12114* (MO, US). **Paraná:** Jaguariaiva, *Dusén 18006* (BM, G, MO, SI). **Rio Grande do Sul:** São Gabriel, *Araujo 345* (US). **Roraima:** Campos Gerais da Região de Caracarahy, *Fróes 23626* (US). **Santa Catarina:** Chapecó, 9 km W of Campo Eré, *Smith & Klein 11529* (US). **São Paulo:** campos d'Ipanema, *Glaziou 13334* (P, US). COLOMBIA. **Arauca:** 13 km al S de Arauca, laguna El Venero, *Joergensen 52* (COL). **Bolívar:** Cerro San Lucas, *Drew E-747* (US). **Boyacá:** Llanos Orientales, El Yopal al S del Hato Matapantano, *Blydenstein & Saravia 1188* (COL). **Magdalena:** Santa Marta, *Smith 142* (BM, K, MO, US). **Meta:** Llanos Orientales, límite de la selva de Arauca, *Blydenstein 736* (COL). **Norte de Santander:** Los Estoraques, La Playa, *Balick 126* (COL). COSTA RICA: **Puntarenas:** 3 km N of the Carretera Interamericana along the road to Boruea, *Pohl et al. 11594* (US). DOMINICAN REPUBLIC. **Dajabón:** Cordillera Central, 6 km de Partido al W en la carretera a Dajabón, *Zanoni et al. 31952* (US). **Monte Cristi:** Sabaneta, Leonor, *Valeur 498* (MO, US). HAITI. Circa Carrajal, *Holdridge 1858* (MO, US). **du Nord:** vicinity of St. Michel de l'Atalaye, *Leonard 7537a* (US). EL SALVADOR. **San Salvador:** Volcán de San Salvador, *Calderón 2272* (US). GUATEMALA. **Jalapa:** between Monjos and Jalapa, about 10 mi. S of Jalapa, *Steyermark 32212* (US). HONDURAS. **Comayagua:** Siguatepeque, *Clewell 3514* (MO). **El Paraíso:** road to Danlí, *Swallen 11226* (MEXU, US). **Francisco Morazán:** 4 km by road SE of Rio Agua Caliente, near Minas de Oro, *Pohl & Gabel 13850* (MO). MEXICO. **Chiapas:** near Caucua, *Nelson 3424* (US); Mun. Villal Corzo, above Colonia Vincente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54586* (MEXU). **Oaxaca:** Distr. Inquila, *Conzali 4364* (MEXU, US). PANAMA. **Coclé:** between Paso de Arado and Olá, *Pittier 5020* (US). **Panamá:** ca. 10 km SW of San Carlos along the Inter-American Hwy., *Davidse & D'Arcy 10126* (MO). **Veraguas:** on Santiago–Santa Fe rd., 18 km S of Santa Fe, *Nee*

8166 (MO). PARAGUAY. **Alto Paraguay:** Fuerte Olimpo, *Anisits 2047* (P). **Amambay:** cerca y al sur de Bellavista, *Fernández Casas & Molero 6335* (G); in regione calcarea cursus superioris fluminis Apa, *Hassler 11058* (BM, G, K, P, US, W). **Caaguazú:** Caaguazú, *Hassler 9259* (BM, G, K, LIL, MO, P, W). **Caazapá:** Tavaí, *Basualdo 2162* (FCQ, MO, SI). **Central:** Tarumandy, *Schinini 6207* (G, LIL, SI, US). **Cordillera:** Barrerito, *Anderson 1120* (US). **Guairá:** Villa Rica, *Joergensen 4568* (BM, MO, SI, US). **Itapúa:** Isla Yaciretá, 6 km de la Ea. Melgarejo, *Quintana et al. 165* (SI). **Misiones:** San Ignacio, *Burkart 18242* (SI). **Paraguarí:** Cerro Peron, prés de Paraguarí, *Balansa 89* (BM, G, K, P, US); Cordillera de Altos, *Fiebrig 664* (BM, G, K, P, SI, US, W). VENEZUELA. **Aragua:** between S. Juan de los Morros and Uberito, *Pittier 11326* (US). **Barinas:** 16 km SW of the Mérida intersection just outside of Barinas, *Davidse 3165* (MO). **Bolívar:** Hato Divina Pastora, *Tamayo 2881* (US). **Carabobo:** Valley of Vijirima, near Guacara, *Pittier 8169* (US). **Cojedes:** 21 km W of San Carlos along Hwy. 5, *Davidse 3140* (MO). **Distrito Federal:** Caracas and vicinity, *Bailey & Bailey 112* (US). **Lara:** Dpto. Palavecino, between the quebrada La Mata and the E side of the Parque Nacional Terepaima, *Burand Jr. & Gantaume V0495* (MO). **Miranda:** Colonia Tovar, *Escalona et al. V274* (MO). **Portuguesa:** Dpto. Guanare, terrenos de la UNELLEZ, *Ramírez 1789* (MO).

25. Paspalum trachycoleon Steudel, Syn. Pl. Glumac. 1: 28. 1855 [1853]. TYPE: Venezuela. Valencia, 9 Oct. 1843, *H. C. Funck 742* (holotype, P!; isotypes, BM!, K!, G!, P!, US-80059!, W!). Figures 24, 25.

Shortly rhizomatous perennial; culms erect to decumbent, (0.8–)1–2 m tall, 0.3–0.6 mm diam., branching at the middle and upper nodes; internodes 5–15 cm long, terete, glabrous, rigid, hollow; nodes pilose to glabrous, brown. Sheaths usually longer than the internodes, overlapping, pubescent to papillose-pilose at the upper portion. Ligules 2–3 mm long, membranous, glabrous; pseudoligule absent. Leaf blades linear-lanceolate, 10–20 cm long, 0.5–1.5 cm wide, flattened, pubescent to papillose-pilose on both surfaces, otherwise glabrous, the base attenuate and the apex acute. Peduncles terminal, partially exserted, pilose. Terminal inflorescences 5–17 cm long, 3–5 cm wide; main axis 3–11 cm long, pilose; racemes 4 to 12, ascendent, divergent, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 3–10 cm long, 4–6 mm wide, foliaceous, green to purple, with a pubescent keel and anastomosed veins on the wings, glabrous, ending in a naked point; pedicels unequal, hispid, laterally inserted in the spikelets; spikelets paired, densely arranged in 4 series. Spikelets ellipsoid, 2.3–3.5 mm long, 1–1.1 mm wide, pale, pilose, with an annular thickening at the base. Upper glume as long as the spikelet, acute to acuminate, hyaline to membranous, the margins pilose with white hairs, a few of them up to 3 mm long, densely pilose toward the base, otherwise glabrous, 3-nerved. Lower lemma as long as the upper glume, acute, membranous, sulcate and with conspicuous nerves, 3-nerved, pilose at the upper portion, otherwise glabrous. Upper anthecium ellipsoid, 2–3.1 mm long, 0.8 mm wide, plano-convex, membranous; upper lemma with simple papillae and bicellular microhairs all over the surface and a tuft of apical macrohairs; upper palea with simple papillae and bicellular microhairs toward the distal portion; lodicules 2, reduced; stamens 3, anthers 1.3–1.4 mm long; stigma plumose. Caryopsis not seen.

Chromosome number. n = 20 (Davidse & Pohl, 1974).

Distribution and habitat. From southern Mexico, Guatemala, Honduras, and El Salvador to Venezuela, Colombia, and central and southern Brazil. It grows in mountain savannas, on dry mountain slopes, between 500 and 2000 m.

Paspalum trachycoleon is close to *P. phyllorhachis* in its similar habit and inflorescence type, which is distinguished by its glabrous spikelets. It is also related to *P. heterotrichon*, but the latter has the rachis of the racemes 3.5–4 mm wide and spikelets solitary.

The specimen *Killip & Smith 19038* has spikelets 3.8–4 mm long.

Representative specimens. BRAZIL. **Distrito Federal:** Reserva Ecológica do IBGE, *da Silva 2659* (MO); near Ribeirão Torto, NE of Lagoa Paranoá, *Irwin et al. 15347* (K, MO). **Goiás:** Niquelândia, *Filgueiras 3567* (SI); without locality, *Burchell 7061-2* (K), *Gardner 4390* (BM, G, K, P). **Minas Gerais:** without locality, *Glaziou 20079* (K). COLOMBIA. **Cundinamarca:** without locality, *without collector 80* (US-1574261). **Huila:** este de Neiva, Cordillera Oriental, *Rusby & Pennell 1014* (US). **Norte de Santander:** Los Estoraques, La Playa, *Balick 127* (COL). **Santander:** Bucaramanga and vicinity, *Killip & Smith 16192* (US); vicinity of Charta, *Killip & Smith 19038* (US). EL SALVADOR. **Copán:** 3 km NW of Copán, *Williams et al. 42957* (US). **San Salvador:** Volcans of San Salvador, *Hitchcock 8946* (US). GUATEMALA. **Zacapa:** slopes of Monte Virgen, *Steyermark 42586* (US). HONDURAS. **El Paraíso:** near 2 km road to Yuscarán, *Swallen 11353* (MEXU, MO, US). **Francisco Morazán:** Rio de Gallo, near El Jicarito, *Swallen 10993* (MEXU, MO, US). **Olancho:** Jutiapa Forest Camp, *Pohl & Gabel 13761* (MO). MEXICO. **Chiapas:** Mun. Cintalapa, 23 km W of Las Cruces along road to La Mina Microwave Station, *Breedlove & Davidse s.n.* (MEXU-830597); Mun. Villa Corzo, above Colonia Vincente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54564* (MEXU). VENEZUELA. **Anzoátegui:** Distr. Libertad, road from El Vigia to Buenos Aires, *Davidse & González 19487* (MO). **Aragua:** de Maracay a Alto, *Croat 21469* (MO). **Distrito Federal:** Caracas, *Bailey & Bailey 447* (US). **Lara:** Distrito Jimenez, entre Alto del Viento y Cerro Pando, *Davidse & González 21162* (SI). **Miranda:** Sebastopol, *Badilla 100*

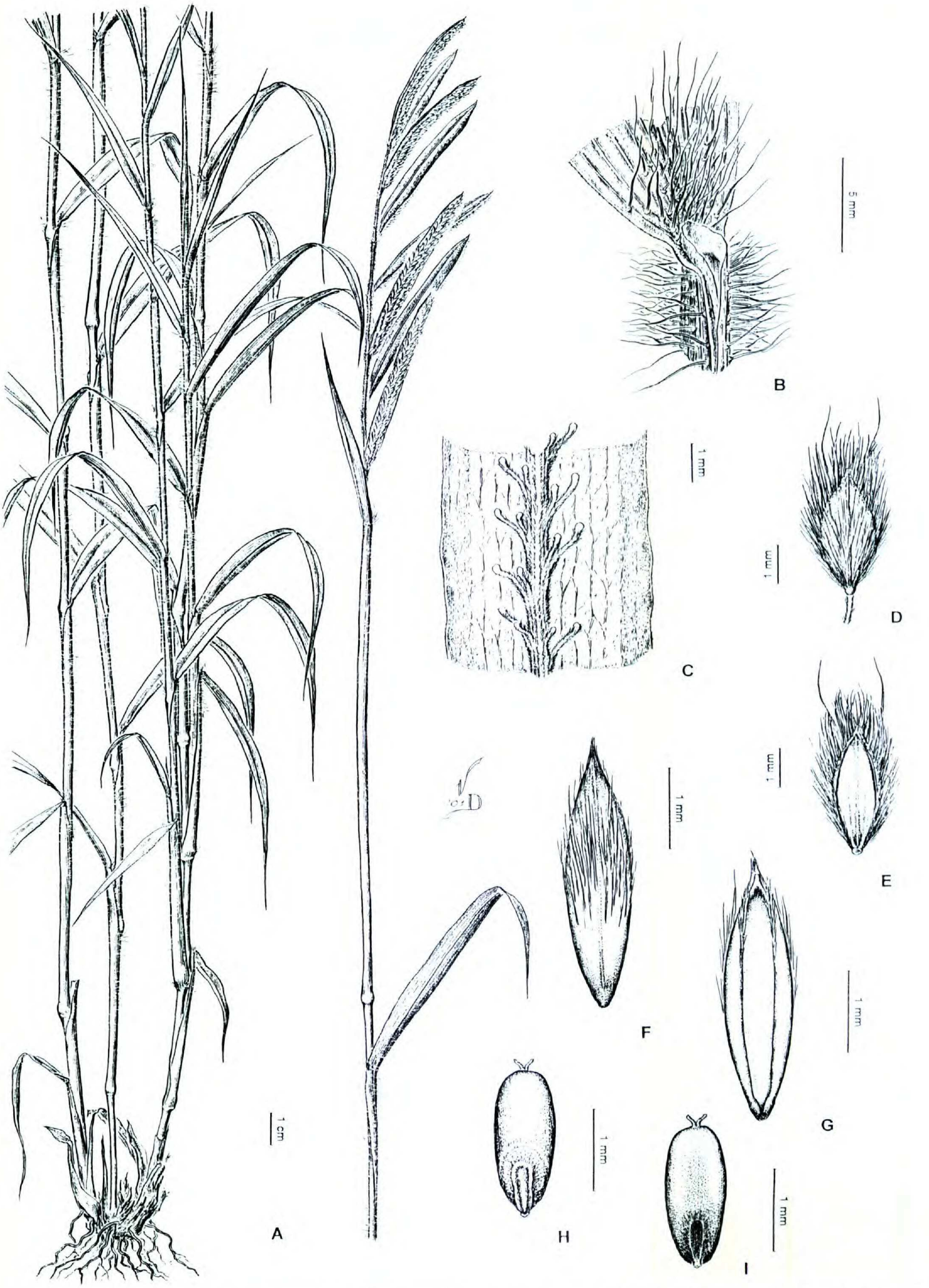

Figure 24. *Paspalum trachycoleon*.—A. Habit. —B. Detail of ligule. —C. Portion of rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (A based on *Davidse & Tillet 4514*, MO; B–I based on *Tamayo 1084*, US.)

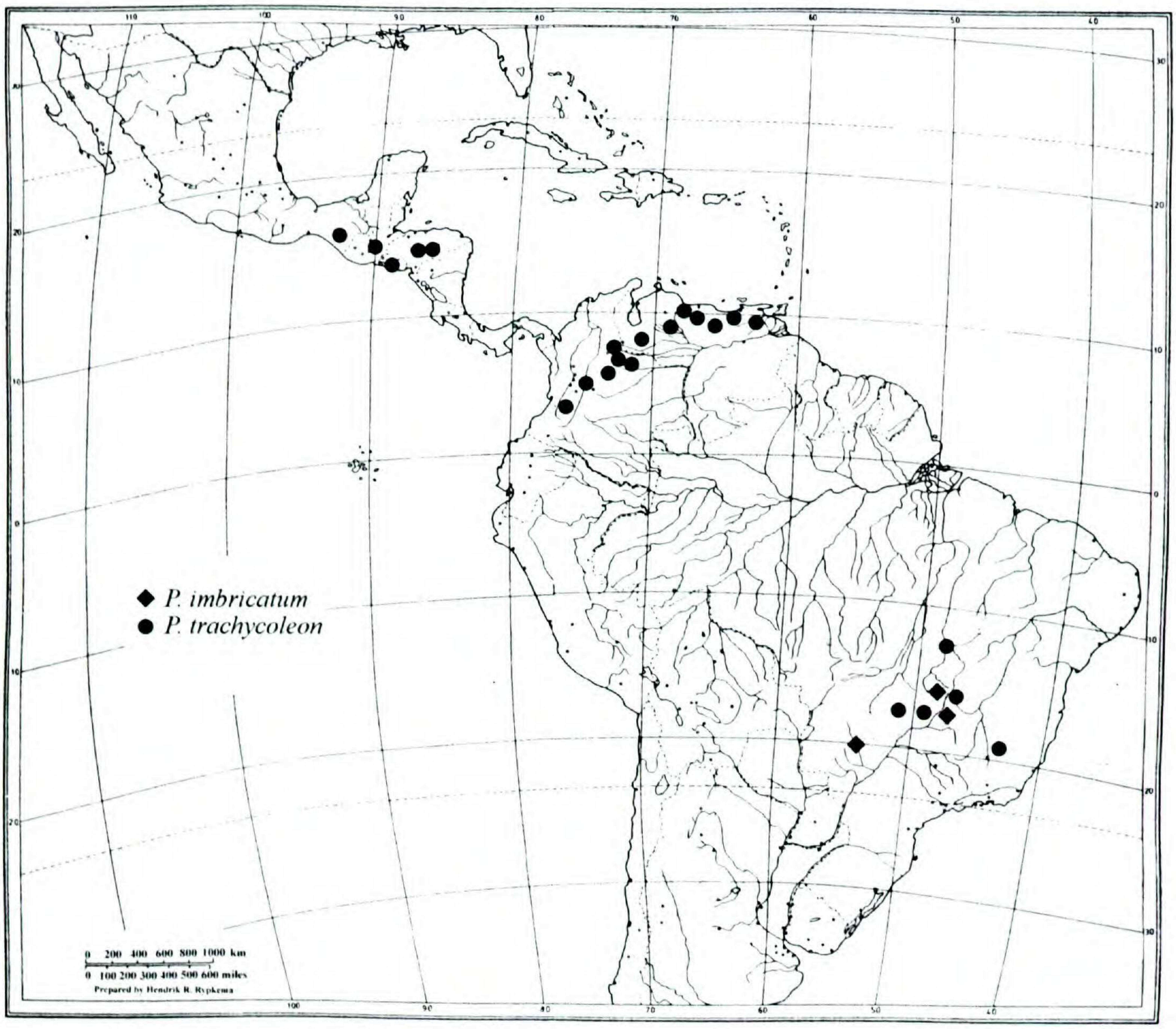
◆ P. imbricatum
● P. trachycoleon
0 200 400 600 800 1000 km
0 100 200 300 400 500 600 miles
Prepared by Hendrik R. Rypkema

Figure 25. Distribution of *Paspalum imbricatum* and *P. trachycoleon.*

(US); San José de Morros, *Davidse & Tillet 4514* (MO). **Monagas:** S-facing mountain slope directly N of Caripe, *Pursell et al. 8580* (US). **Without department:** Barrancas, *Tamayo 1084* (US); Los Venados, *Tamayo 2046* (US).

EXCLUDED SPECIES

Paspalum sanguinolentum Trin. was placed in the subgenus *Ceresia* by Chase (1929), but this species belongs to subgenus *Paspalum*, group Eriantha.

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Appendix 1

List of accepted species of *Paspalum* subg. *Ceresia*.

1. *Paspalum aspidiotes* Trin.
2. *P. biaristatum* Filg. & Davidse
3. *P. buchtienii* Hack.
4. *P. burmanii* Filg., Morrone & Zuloaga
5. *P. cachimboense* Davidse, Morrone & Zuloaga
6. *P. carinatum* Humb. & Bonpl. ex Flüggé
7. *P. ceresia* (Kuntze) Chase
8. *P. cordatum* Hack.
9. *P. cymbiforme* E. Fourn.
10. *P. eucomum* Nees ex Trin.
11. *P. goyasense* Davidse, Morrone & Zuloaga
12. *P. heterotrichon* Trin.
13. *P. humboldtianum* Flüggé
14. *P. imbricatum* Filg.
15. *P. lanciflorum* Trin.
16. *P. longiaristatum* Davidse & Filg.
17. *P. malmeanum* Ekman
18. *P. niquelandiae* Filg.
19. *P. pectinatum* Nees ex Trin.
20. *P. petrense* A. G. Burman
21. *P. phyllorhachis* Hack.
22. *P. polyphyllum* Nees ex Trin.
23. *P. reticulinerve* Renvoize
24. *P. stellatum* Humb. & Bonpl. ex Flüggé
25. *P. trachycoleon* Steud.

Appendix 2

Index to exsiccatae. Each specimen is alphabetically listed by the first collector. The number in parentheses refers to its associated species (see Appendix 1). An asterisk (*) indicates a voucher for the SEM study.

Abraham 83 (6); Acosta Solís 21454 (13); Ahumada 3541 (24); Alba 53–23 (19), 53–96 (6); Allem 1558 (6), 2007 (6), 2236 (24); Almeida 572 (19); Alston 7569 (19); Amat 3 (15); Anderson 1120 (24), 8286 (24), 9413 (22), 9421 (24), 9969 (6), 10304 (22), 35213 (19), 35798 (22); Anisits 2047 (24); Araujo 104 (19), 144 (22), 345 (24); Archer 629 (13), 3843 (24), 4995 (22); Arechavaleta s.n. (22); Argent 6460 (22), 6766 (19); Aristeguieta 238 (25), 4219 (6); Arsène 2813 (13); Asplund 6531 (13), 7593 (13), 10498 (13), 10633 (19), 12014 (13); Aynard 6019 (6).

Badilla 100 (25); Bailey 112 (24), 447 (25); Balansa 89 (24), 90 (22), 90a (22), 126 (24), 127 (25); Balick 127 (25); Balls 6923 (13); Bang 265 (3); Barbosa 3018 (19), 3032 (19); Barclay 5703 (13); Barlow 30/1173 (19); Barreto 46 (24), 529 (22), 1483 (22), 1577 (24), 2952 (19); Basualdo 2162 (24); Beck 4025 (7), 8714 (3), 12330 (24), 19948 (3), 20552 (19), 20564 (6); Bentacur 1510 (19); Berro 2680 (22); Bertoni 5406 (24); Black 47–1777 (6), 51–12029 (19), 51–12148 (22), 51–12291 (6); Blake 7445 (19); Blydenstein 734 (19), 736 (24), 847 (6), 856 (19), 900 (19), 939 (8), 1037 (19), 1082 (6), 1188 (24), 1468 (15), 1562 (19); Boelcke 16646 (13); Borges 189 (22); Brade 19638 (8), 20377 (22); Breedlove 3313 (13), 13822 (9), 20498 (9), 39106 (9), 42481 (25), 53954 (24), 54362 (12), 54468 (25), 54564 (25), 54586 (24), 54596 (12), s.n. (25); Brooks 70 (24), 125 (7), 144 (16); Bruderreck 2 (6); Buchtien 447 (3), 3629 (3), 4274 (3), s.n. (3); Burandt, Jr. V0495 (24), V0530 (12); Burchell 4329 (22), 4574 (22), 4681 (22), 5769 (22), 7061–2 (25), 7124 (25), 7295 (25); Burkart 5335 (13), 10211 (13), 11014 (13), 16984 (13), 18242 (24), 21610 (24); Burman 393 (24).

Caballero Pardo 77 (7); Cabrera 2278 (8), 22730 (7), 28254 (24); Calderón 2272 (24), 2708 (8), 2760 (1); Callejas 6886 (15); Calzada 17051 (19); Camp E-2743 (13), 2332 (7); Capell s.n. (22); Cárdenas 515 (13), 3410 (13), 3606 (22); Carnevali 1083 (24), 3124 (24), 3200 (22), 3379 (24); Castellanos 17922 (22), 17957 (22); Cavalcante 2131 (23); Chase 1239 (24), 8337 (22), 8975 (21), 9100 (24), 9148 (22), 9212 (19), 9250 (19), 9253 (24), 9295 (24), 9308 (24), 9325 (21), 9352 (22), 9367 (22), 9369 (22), 9559 (22), 9917 (22), 10230 (19), 10249 (19), 10276 (19), 10306 (6), 10350 (19), 10595 (6), 10655 (19), 10740 (22), 10872 (24), 10907 (24), 11200 (10), 11543 (24), 11549 (22), 11602 (22), 11768 (24), 11962 (17), 12014 (24), 12028 (24), 12085 (25), 12088 (24), 12114 (24), 12292 (25), 12294 (13); Chávez 3217 (7); Chaviel 450 (1); Claussen s.n. (24); Clayton 4631 (8), 4804 (6); Clewell 3514 (24); Conzali 4364 (24); Coradin 696 (6); Costa Sacco 133 (22); Croat 21469 (25); Cuatrecasas 3001 (13), 7649-A (19), 25702 (13).

D'Arcy 141 (22), 2271 (22), 2659 (25), 4082 (6), 13527 (15); Daly 2171 (22); Daniel A-2 (19), 60 (6); Davidse 3065 (25), 3082 (12), 3140 (24), 3165 (24), 4073 (13), 4514 (25), 4615a (6), 4708 (1), 5109 (19), 5242 (19), 5321 (19), 5597 (13), 10126 (24), 10655 (22), 10967 (22), 10985 (22), 11028 (22), 11123 (22), 11148 (22), 11308 (22), 11316 (22), 11380 (22), 11401 (22), 11407 (22), 12087 (6), 12124 (6), 12158 (25), 12159 (24), 12276 (24), 14176 (19), 15652 (19), 16117 (19), 16775 (6), 16942 (6), 18355 (6), 19314 (15), 19317 (6), 19487 (25), 19802 (6), 20544 (19), 21162 (25), 21312 (25), 21370 (13), 22647 (15), 22944 (1), 28159 (13), 31637 (9), 35448 (13); Dawson 14142 (24), 14215 (24), 14863 (25); de Campos 192 (22); de Jesus 3 (10), 16 (24); de Lima s.n. (22); de Paula 65 (24); Dedecca 302 (22); Dias 67 (10); Dinelli 12876 (7); Dombrowski 780 (19), 4570 (22), 5984 (22), 6488 (19), 6715 (19), 9037 (19), 9784 (19); Drew E-747 (24); Dusén 26a (22), 283 (22), 2770 (19), 2844 (19), 2844a (19), 3657 (22), 3659 (22), 4023 (24), 8011 (24), 9109 (8), 10412 (6), 10611 (19), 10613 (19), 13256 (19), 13805a (22), 14489 (22), 15727 (19), 16057* (19), 16174 (8), 17388a (22), 17407 (19), 17934 (6), 18006 (24), 18065 (10), s.n. (22); Dutra 464 (22).

Echeverry 1251 (13), 2312 (15); Eggler 639 (9); Egler 1262 (15); Eiten 3777 (7), 4417 (24), 4418 (7), 6746 (19), 6760 (19), 7626 (22), 9151 (19); Ekman 594 (24), 596 (24), 2274 (12), 2302 (24), 2401 (12), 2484 (24), 13404 (12), 14018 (12); Ellenberger 1369 (22); Enamorado 23 (9); Escalona V274 (24); Eskuche 4556 (22).

Fassett 25502 (13); Felippone 6462 (22); Fendler 1697 (25), 1698 (12), 2533 (24); Fernández 89 (24); Fernández Casas 6335 (24); Ferreyra 5373 (13); Fiebrig 664 (24), 2664 (7), 3082 (13), 4970 (24), 4978 (24), 6222 (22); Filgueiras 2131 (14), 2184 (14), 2280 (7), 2342 (16), 2408 (2), 2409 (2), 2455 (19), 2477 (4), 2780 (16), 3260 (22), 3392 (16), 3317 (14), 3567* (25); Filipovich 398 (13);

Flores Flanco 3643 (13); Fonseça 224 (2), 227 (16), 600 (22); Fontana 114–5 (24); Fraser 370 (1); Freytag s.n. (24); Fróes 23626 (24); Funcke 742 (25).

García Barriga 4993 (19), 21426 (15); Gardner 4030 (24), 4390 (25); Gentry 15081 (19), 71186 (24); Gifford G-101 (15); Giraldo-Cañas 2566 (6), 2631 (19); Glaziou 2260 (22), 4309 (22), 6775 (22), 7980 (22), 13334 (24), 16548 (22), 17406 (10), 17410 (22), 17411 (22), 17414 (24), 17940 (22), 18607 (22), 18644 (22), 18674 (22), 20070 (21), 20076 (21), 20078 (21), 20079 (25), 20082 (22), 20083 (22), 20084 (15), 22427 (19), 22437 (22), 22441 (11), 22443 (11), 22544 (15), 22544b (14), 22545 (24), 22546 (24), 22547 (6), 22549 (24), 22551 (10), 22553 p.p. (24), 22555 (10), 22556 (6), 22557 (24), 22558 (22), 22559 (22), 22560 (22), 22561 (22), 22562 (22), 22576 (12), 22577 (25), 22949 (24), s.n. (24); Goés s.n. (22); Goodland 923 (15); Gottsberger 1043 (10); Graham 520 (19); Grignon 84257 (13); Guala 1320 (24), 1450 (22); Guánchez 3618 (1); Gutiérrez 655 (17).

Haase 630 (19); Hahn 5592b (15); Handro 97 (22); Harley 10330 (19), 10480 (19), SH209 (22); Hassler 1039 (24), 1058 (24), 9259 (24), 9261 (22), 9261a (22), 9380 (22), 10209 (22), 11058 (24), 11501 (22), 11561 (22), 11916 (22); Hatschbach 5461 (22), 6864 (22), 7751 (22), 8965 (22), 11110 (22), 12097 (8), 16134 (22), 25048 (19), 25264 (19), 32479 (19), 33152 (19), 44562 (22), 45697 (19), 47650 (24), 48811 (19), 64890 (22), 66698 (22); Haught 2709 (19); Hazlett 994 (24); Heithanus 163 (19); Heringer 4615 (15), 7249 (22), 7382 (14), 10432 (22); Hermann 10995 (19), 11089 (19); Hernández 2283 (19); Hernández Xolocotzi X-623 (12); Herter 1755 (22); Heyde 6271 (13); Hicken s.n. (24); Hill 1548 (19); Hinton 1440 (13), 2532 (9), 11400 (13); Hitchcock 6355 (13), 6837 (13), 7055 (13), 7297 (13), 8186 (13), 8297 (12), 8946 (25), 21306 (13), 21710 (13), 22830 (13); Holdridge 1858 (24); Holway 98 (22), 1633 (22), 1672 (22), 1708 (24); Hostmann 1306 (6); Huber 9643 (1), 9898 (1); Hunt 5550 (24), 6012 (22), 6246 (22); Hutchinson 4495 (13), 5194 (7).

Ibarrola 2834 (24); Idrobo 11636 (13); Iltis 342 (13); Imaguire 605 (22); Irwin 739 (6), 5163 (24), 5171 (22), 5647 (22), 5800 (22), 6205 (22), 6579 (19), 6758 (19), 6806 (19), 7069 (22), 7219 (22), 8001 (24), 9495 (22), 9648 (11), 9658 (11), 10044 (22), 10257 (11), 10654 (11), 10737 (11), 13034 (14), 13241 (14), 15177 (24), 15328 (10), 15347 (25), 15928 (24), 15929 (24), 16232 (22), 16232a (22), 16465 (24), 17256 (22), 17314 (24), 17617 (24), 17854 (22), 17967 (22), 19486 (22), 27667 (6), 28353 (22); Isabell s.n. (7).

Jangoux 10153 (19); Joergensen 1765 (13), 2882 (24), 4568 (24); Joly 1456 (24); Jorgensen 52 (24); Jürgens G-299 (22).

Killeen 687 (24), 904 (24), 1795 (22), 1952 (24), 1998 (24), 2011B (24), 2024* (17), 2076 (17), 2458 (24), 2473 (24), 2474* (24), 2477 (24), 2478 (17), 2487 (24), 2782a (19), 2795 (22), 2823 (6), 4152 (7), 4824 (23), 4929 (15), 6056 (24), 6541 (23); Killip 4555 (12), 16192 (25), 19038 (25), 19770 (13), 34321 (19); Klein 3916 (19); Koninck 157 (25); Kral 69245 (19), 72050 (1), 75939 (11); Krapovickas 14972 (24), 25202 (24); Kuhlmann 1667 (17), 1668 (17), 1671 (23), 1674 (15), s.n. (22); Kummrow 2204 (22).

Lazor 3350 (19); Leavenworth 1649 (13); Lehmann 979 (19); Leonard 7526 (24), 7537a (24), 7793 (12), 8953 (12), 8957 (12); Liebmann 225 (9); Liesner 19350 (15); Lima 58–3056 (24); Linares 3663 (9), 3904 (9); Linden 1555 (25); Llano 47 (6); Llatas Quiroz 2322 (13); Loefgren 2331 (22).

Macedo 351 (10), 1121 (12), 1543 (8); Machado de Campos 111 (19); Machuca Nuñez 4640 (13); Magalhães 101 (22), 908 (21), 19226 (24); Maguire 32038 (15); Malme 965 (22), 1562b (12), 2226 (22), s.n. (22); Mandon 1254 (13); Marin 851 (13); Martius 267 (22); Martínez F-1953B (13); McVaugh 19098 (13); Mendoça 2293 (22); Mereles 2943 (24); Mexía 5519 (24); Meyer 2090 (22), s.n. (24); Miranda 3883 (24); Molina 8702 (25), 12041 (13), 13177 (24); Montes 1943 (22), 1953 (24), 1959 (22), 14920 (24), 15353 (24), 16250 (24), 16409 (24), 27642 (24); Montoro s.n. (22); Moraes 1713 (24); Moran 5505 (12); Mori 13303 (22), 17298 (6); Moritz 1537 (25); Morrone 205 (24); Mostacedo 314 (7), 1783 (23), 1862 (1); Müller 2036 (13); Mutis 5453 (19), 5537 (13); Myers 3338 (19), 3404 (24).

Nee 8166 (24), 26848 (3), 40372 (7), 46904 (19), 49412 (22); Nelson 3424 (24); Nicora 4700 (22), 4708 (24), 6352 (24); Niederlein 570 (22); Norrmann 159 (24); Núñez 7175 (13).

Oldenburger 5 (15); Oliveira 305 (7), 598 (7), 615 (2), 623 (2), 630 (2), 638 (16), 700 (16), 719 (12), 758* (2), 763 (19); Øllgaard 90721 (7); Orozco 182 (19); Orth 1059 (22); Osten 6632 (22).

Parodi 2412 (22), 4664 (24), 7070 (24); Partch 69–91 (13); Pedersen 1032 (22), 2611 (24), 3783 (24), 11677 (22), 13371 (22), 15713 (24); Pennell 8174 (19); Perdonnet 496 (22); Peterson 9478 (7), 11887 (22), 11891 (24); Pinheiro 142 (7), 517 (7), 625 (7); Pinto 796 (19), 894 (19), 1066 (19), 1141 (19), 1467 (19), 1550 (19); Pire 14649 (24); Pires 2290 (24), 16684 (24); Pittier 214 (25), 1788 (25), 4351 (19), 5020 (24), 5902 (25), 6033 (25), 7487 (24), 7489 (24), 8169 (24), 9734 (13), 11326 (24), 11998 (24), 12818 (25); Plowman 8949 (23), 9133 (23), 19132 (15); Pohl 714 (19), 1454 (15), 2833 (24), 11594 (24), 12274 (6), 12361 (19), 13531 (9), 13761 (25), 13850 (24), 13922 (19); Porter 4300 (19); Prance 13823 (1); Purpus 2002 (13); Purseglove 6514 (6); Pursell 8580 (25).

Quarín 2235 (24), 3340 (24), 3716 (24), 3852 (24), 4043 (24); Quintana 165 (24); Quiroga 38 (24).

Rambo 40511 (22), 40690 (22), 40804 (22), 53906 (22), 54017 (22), 54991 (22); Ramia 1009 (24); Ramirez 961 (15), 1789 (24); Ramos 182a (6); Ratter 520 (22), 820 (24), 1915 (24), 1969 (19), 2883 (24), 2884 (25), 3335 (24); Reeder 3313 (13); Reeves 194 (25); Regnell III-1345 (25), III-1344 (24), III-1335 (19), I-466 (22); Reineck 431 (22); Reitz 10652 (22), 10659 (22), 10681 (22), 10906 (22), 10933 (22), 12477 (22); Renvoize 3870 (7), 4038 (13), 4048 (22), 5409 (19); Riedel 966 (12), 1043 (22), 1048 (1), 2143 (22), s.n. (1), s.n. (12), s.n. (19), s.n. (22), s.n. (24); Rivera L-L41 (19), 3 (19); Rizzo 4285 (22); Robinson 3189 (22); Rodrigues 662 (6); Rodríguez 206 (24); Rojas 2757 (24), 9569 (22), 13404 (22), 13933 (22); Romanczuk 112 (24); Rombouts 308 (19); Rondon 2135 (6), s.n. (15), s.n. (24); Rosengurtt B-3197 (22), B-5749 (24), B-5750 (22), B-5883 (24), B-7397 (22); Rueda 1200 (9); Rusby 1014 (25); Rzedowski 17636 (13).

Sánchez Vega 2332 (7), 2341 (13); Santos 1701 (24); Saravia 4006 (13), 4186 (22), 4215 (22), 12315 (22); Schaffner 120 (13), 154 (13); Schenck 3155 (22); Schinini 1323 (24), 1403 (24), 1436 (24), 6207 (24); Schmidt 53 (22), 136 (13); Schreiter 9251 (13), 9256 (7); Schulz 300 (24), 7220 (24), 17275 (22); Schwacke 8444 (22); Schwarz 2214 (22), 5539 (24), 5703 (24), 10003 (24), 10161 (24); Sellow 1232 (19), 1239 (19), 1240 (22), 4416 (22), 5686 (24), s.n. (19), s.n. (22), s.n. (24); Semir 380 (19); Semple

150 (19); Sendulsky 1239 (10); Sermeño s.n. (13); Shaw s.n. (19), s.n. (6); Silva 114 (24); Smith 142 (24), 143 (12), 2170 (25), 5907 (22), 6316 (22), 6912 (24), 8445 (19), 11529 (24), 12013 (22), 12106 (22), 14462 (6), 14579 (8), 14858 (8), 15569 (19), 16123 (22); Soderstrom 1124 (6); Sohns 427 (13); Soria 4442 (24); Soriano 986 (13); Souza 5548 (7); Spegazzini s.n. (22); Standley 13185 (12), 56275 (24); Steinbach 3015 (3), 3712 (22), 5162 (22), 5385 (22), 6618 (13), 6808 (22), 7103 (24); Stevens 24761 (13), 25701 (13); Steyermark 29550 (9), 32312 (24), 42586 (25), 55152 (25), 59150 (19), 75259 (19), 121984 (25), 127710 (24), 127714 (25); Stockwell 893 (13); Stuckert 14159 (13), 18694 (22); Swallen 3074 (19), 3643 (6), 3687 (6), 3772 (7), 4029 (15), 4078 (6), 4762 (6), 8344 (19), 8361 (22), 8477 (19), 8486 (22), 8518 (22), 8584 (22), 8613 (22), 8639 (22), 8698 (22), 8772 (22), 8784 (22), 8932 (22), 8975 1/2 (22), 8994 (22), 9033 (22), 9083 (22), 9087 (22), 9132 (22), 9150 (22), 9159 (22), 9181 (22), 9540 (24), 9590 (24), 10747 (9), 10809 (9), 10810 (12), 10993 (25), 11226 (24), 11353 (25), 11354 (12), 11401 (12).

Tablas 738 (13); Tamayo 1084 (25), 1867 (22), 2046* (25), 2281 (13), 2881 (24), 3198 (15), s.n. (15); Tate 157 (15); Tenorio 16710 (13); Texeira 1197 (1); Torrico 331 (7); Tovar 1005 (13), 1020 (7), 4176* (12); Triana 761 (25); Troncoso 3387 (24).

Ule 7919 (24), 8032 (24).

Valeur 498 (24); Valls 8340 (6); van der Werff 7863 (22); Vargas 2459 (7), 19047 (7); Venturi 8320 (7), 9905 (7); Vieira 54 (22); Villa Carenzo 1818 (13); Vincelli 1146 (19).

Warming s.n. (25); Webster 29732 (19); Weddell 1699* (8), 2556 (10); Widgren s.n. (22), s.n. (19); Williams 10533 (24), 13088 (15), 14704 (24), 17344 (24), 42957 (25); Wood 4273 (22), 4306 (25), 7852 (13); Wurdack 27 (15).

Zardini 26848 (24), 51117 (19); Zanoni 31952 (24); Zuloaga 888 (22), 910 (24), 2383 (22), 3835 (11), 3839 (19), 4379 (6), 4413 (15), 4587 (22), 4606 (22), 4654 (22), 4697 (22), 4874 (22), 4904 (22), 4930 (22), 5371 (24), 5671 (24), 5788 (24), 5791 (22), 5885 (13), 6585 (22), 6817 (24), 6944 (22).

APPENDIX 3

List of specimens for outgroup taxa in the cladistic analysis.

Anthaenantiopsis fiebrigii L. Parodi
ARGENTINA. **Jujuy:** Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Cabrera et al. 32666* (SI).
Panicum
Panicum laxum Sw.
ARGENTINA. **Corrientes:** Monte Caseros, monte del arroyo El Seibo, *Nicora 4516* (SI). **Misiones:** Dep. Iguazú, Cataratas Iguazú, *Cabrera et al. 28942* (SI). **Santa Fe:** Río Paraná, Canal Viejo, *Job 710* (SI).
Panicum obtusum Kunth
U.S.A. **Arizona:** Box Canyon Road, *Gould 2889* (SI).
Paspalum Group Dissecta
Paspalum acuminatum Raddi
ARGENTINA. **Tucumán:** Dpto. Monteros, Loc. Monteros, *Lillo 38377* (SI); Dpto. Leales, Loc. Leales, *Venturi 699* (SI). **Entre Ríos:** Dpto. Feliciano, río Guayquiraró, Ruta 12, *Burkart et al. 23250* (SI).
Paspalum dissectum (L.) L.
U.S.A. **Alabama:** N side of Gulf Shores, *Kral 51314* (MO). **Louisiana:** Cheniere Lake, *Burkunas 605* (MO).
Paspalum Group Eriantha
Paspalum erianthum Nees ex Trin.
BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, Est. Las Madres, *Killeen 1369* (SI). BRAZIL. **Distrito Federal:** Area da Proflora, *Filgueiras & Zuloaga 2207* (SI); Brasília, Lago Sul, *Zuloaga 3836* (SI)
Paspalum guttatum Trin.
BRAZIL. **Distrito Federal:** between Brasília & Sobradinho, *Irwin et al. 9163* (MO). **Goiás:** s.l., *Glaziou 22442* (G).
Paspalum sanguinolentum Trin.
BRAZIL. **Goiás:** 3 km of Cristalina, *Irwin et al. 9858* (MO). **Minas Gerais:** Sierra da Piedade, Santuario, *Zuloaga & Morrone 4676* (SI).
Paspalum Group Notata
Paspalum almum Chase
PARAGUAY. **Central:** Tavarory, 3 km S from administration, 1 km E of río Paraguay, *Zardini & Tillería 29180* (SI); Itá Enramada, *Schinini 6277* (SI). **Pte. Hayes:** Estero Patiño, ruta Trans Chaco, km 164, *Quarín 4049* (SI).
Paspalum cromyorrhizon Trin. ex Döll
ARGENTINA. **Corrientes:** orillas del Timboí, camino de Monte Caseros, *Nicora 4629* (SI). BRAZIL. **Río Grande do Sul:** Centro Agronómico de Guaiba, *Burkart 25051* (SI). URUGUAY. **Durazno:** La Paloma, *Schroeder s.n.* (SI).
Paspalum notatum Flüggé
ARGENTINA. **Córdoba:** Santa María, Alta Gracia, *Hunziker 1178* (SI). **Corrientes:** San Miguel, 19 km S de Caa-Catí, Ruta 5, *Ahumada 1837* (SI); Monte Caseros, orillas del Uruguay, *Nicora 4587* (SI). **Misiones:** Dpto. Apóstoles, Apóstoles, *Burkart 14273* (SI).
Paspalum Group Racemosa
Paspalum candidum (Humb. & Bonpl. ex Flüggé) Kunth
ARGENTINA. **Jujuy:** Dpto. Dr. Manuel Belgrano, faldeo del Cerro Sendero Abra de Lozano, *Deginani & Cialdella 135* (SI); Dpto. Capital, Lagunas de Yala, *Cabrera et al. 30676* (SI); Termas de Reyes, *Burkart et al. 11218* (SI).
Paspalum prostatum Scribn. & Merr.
MEXICO. **Hidalgo:** near Honey Station, *Pringle 8891* (SI). VENEZUELA. **Lara:** Distrito Jiménez, 4–5 km of Sanare, *Davidse & González 21366* (SI).
Paspalum racemosum Lam.
PERU. **Lima:** Chancay, Lomas of Pasomayo, S of Chancay, *Stork & Vargas 9344* (SI). **Trujillo:** La Libertad, Cerro Cabezón, *Sagástegui & Mostacero 10443* (SI); La Libertad, Barraza, *Mostacero & Ramírez 690* (SI).

APPENDIX 4

Index to scientific names. Synonyms appear in italics.

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